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Taxonomic studies in the Labiatae tribe Pogostemoneae

J. R. Press

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Taxonomic studies in the Labiatae tribe Pogostemoneae

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Synopsis

Relationships within the tribe Pogostemoneae (Benth. ex Endl.) Briq. of the family Labiatae are investigated. After a review of the taxonomic history of the group, the distribution of sixty-four morphological characters in 138 species from ten genera is discussed. The CLASP 202 computer program incorporating cluster analyses and ordination methods is used to analyse the morphological data. Discussion of the relationships of supra-specific taxa is followed by an enumeration of the species within each genus.

Close similarities are established between *Comanthosphace* S. Moore, *Leucosceptrum* Smith, and *Rostrinucula* Kudo (formerly included in *Elsholtzia* Willd.). Further investigation into style and fruit characters is required to confirm the status of *Leucosceptrum* as a genus separate from *Comanthosphace*. Close similarities are also established between *Elsholtzia, Keiskea* Miq., and *Tetradenia* Benth. (formerly grouped with *Colebrookea* Smith, *Dysophylla* Blume and *Pogostemon* Desf.). *Elsholtzia* is divided into three sections, one (section *Platyelasma*) being raised from the rank of series. Section *Cyclostegia* is reduced to a synonym of section *Elsholtzia*. The bract and inflorescence characters which are alleged to distinguish them form a transition series between the two sections. Five of the six species of *Keiskea* are compared for the first time, and additional distinguishing characters are given for the genus. *Eurysolen* Prain is included within the tribe Pogostemoneae on the basis of its fruit morphology but its relationships within the tribe remain in doubt. *Dysophylla* is reduced to a section, section *Eusteralis,* of *Pogostemon.* The distinguishing characters form a transition series between the genera. In addition a number of characters formerly used to separate the genera are now believed to be merely responses to aquatic environments. Two new species, *Pogostemon glabratus* and *P. trinervis* are formally described. Sixteen new combinations are made.

1. Introduction

The Pogostemoneae is a tribe containing some 200 species divided among 10 genera. The group has a wide distribution through the warm temperate and tropical regions of the Old World (Fig. 1). Most species are herbs or suffruticose perennials, but some, e.g. species of *Dysophylla*

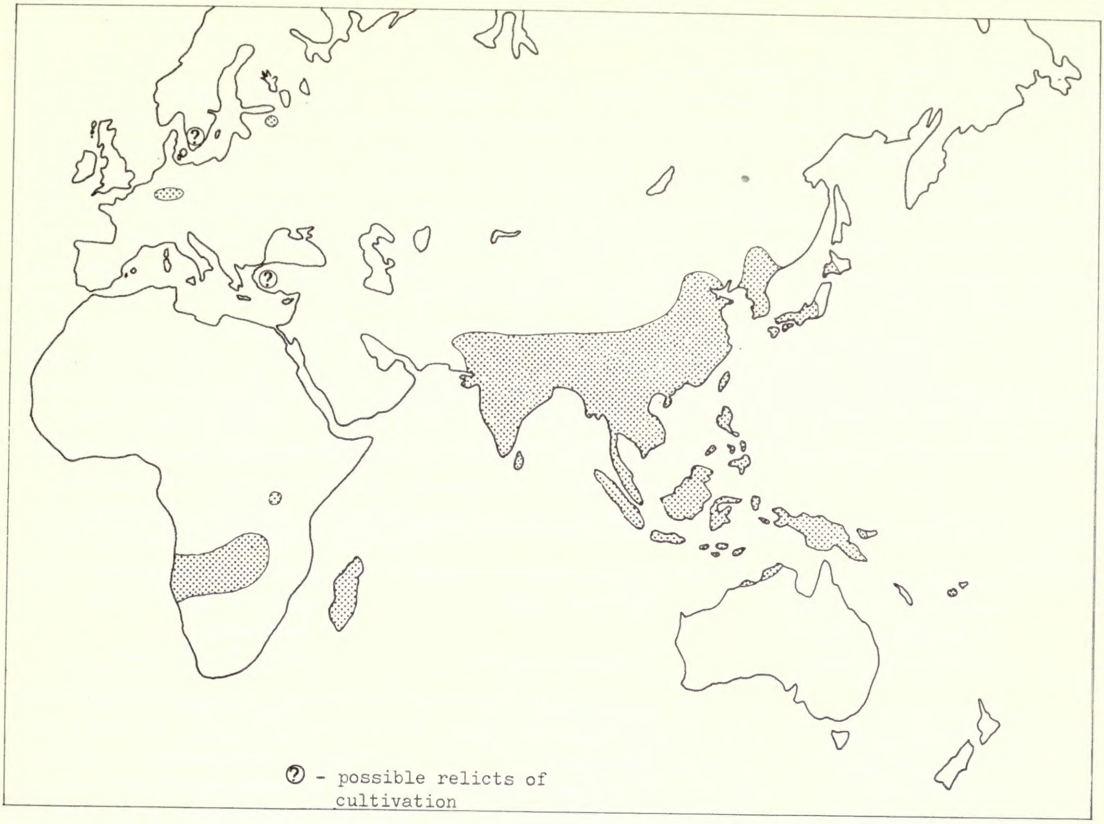

Fig. 1 Distribution of the Pogostemoneae.

Blume, are aquatic or amphibious; a few, e.g. *Elsholtzia fruticosa* (D. Don) Rehder and *Colebrookea oppositifolia* Smith, are shrubs.

Several species, particularly of *Elsholtzia* Willd. and *Pogostemon* Desf., have commercial and homeopathic uses. The most important are *Pogostemon heynianus* Benth., which provides the patchouli oil of perfumery (Day, 1979), and several species of *Elsholtzia,* e.g. *E. ciliata* (Thunb.) Hylander and *E. rugulosa* Hensley, which are used as stomachics and carminatives (Chopra, Nayar & Chopra, 1956; Keys, 1976; Yunnan Xian Weishenju, 1973). A number of other species are used as condiments and in folk-medicine, especially in eastern and south-eastern Asia. *Pogostemon mutamba* (Hiern) G. Taylor (Fig. 30) from southern tropical Africa produces starchy edible tubers (Taylor, 1931). Several species are valuable food sources for bees, e.g. *Pogostemon parviflorus* (Benth.) Benth., from which pangol honey is produced.

This relatively small but quite well-known tribe has been rather neglected by recent workers in the Labiatae. Various genera have been studied in part or in whole and a number of changes suggested, although these sometimes contradict with each other. In particular the generic limits of *Dysophylla*, *Pogostemon*, *Comanthosphace* S. Moore, and *Leucosceptrum* Smith bear further investigation, as do the positions within the tribe of *Keiskea* Miq., *Rostrinucula* Kudo and *Tetradenia* Benth., and the possible inclusion of *Eurysolen* Prain. No recent worker has considered the tribe in its entirety and this is the aim of this study. To ensure a thorough analysis and detailed assessment of all the available data, numerical phenetic methods have been used to investigate the interrelationships and definitions of the different taxa.

2. Historical review

Taxonomic position of the Pogostemoneae

The only complete monographic treatments of the Labiatae are those of Bentham (1832–36, 1848). In his earlier work Bentham (1832–36) divided the family into eleven tribes, and described a number of *ad hoc* groups within them. Endlicher (1838) accepted Bentham's arrangement and also assigned the rank of subtribe to Bentham's unnamed groups. Subtribes Pogostemeae Endl. (containing *Dysophylla* and *Pogostemon*) and Elsholtzieae Endl. (containing *Elsholtzia* and *Tetradenia*) were placed in the tribe Menthoideae Benth. (see Table 1). In his second account Bentham (1848) rearranged his tribes, reduced the number to eight and recognized a number of subtribes. For example, subtribe Elsholtzieae (containing *Colebrookea* Smith, *Dysophylla, Elsholtzia, Pogostemon*, and *Tetradenia*) was placed in the tribe Satureieae Benth. (see Table 1). Later classifications were minor variations of that of Bentham until Briquet (1897) produced an apparently very different classification, with more subdivisions than in the earlier ones. He recognized eight subfamilies, 14 tribes and 11 subtribes (see Table 1). Although Briquet altered much of the order of Bentham's and Endlicher's systems, the essential

Table 1 Summary of the classifications of the Labiatae by Endlicher (1838), Bentham (1848), and Briquet (1897).

	Endlicher, 1838 (based on Bentham, 1832–36) Tribes & subtribes		Bentham, 1848 Tribes & subtribes		Briquet, 1897 Subfamilies, tribes & subtribes
I	Ocimoideae	I	Ocimoideae	I	Ajugoideae
	1. Moschosmeae		3 unnamed divisons		1. Ajugeae
	2. Plectrantheae	II	Satureieae		2. Rosmarineae
	3. Hyptideae		1. Elsholtzeieae	II	Prostantheroideae
	4. Lavanduleae		2. Menthoideae	III	Prasioideae
II	Menthoideae		3. Thymeae	IV	Scutellarioideae
	1. Pogostemeae		4. Melisseae	V	Lavanduloideae
	2. Elsholtzieae		5. Genera anomala	VI	Stachyoideae
	3. Mentheae	III	Monardeae		1. Marrubieae
	4. Meriandreae	IV	Nepeteae		2. Perilomieae
III	Monardeae	V	Stachydeae		3. Nepeteae
	1. Salvieae		1. Scutellarieae		4. Stachydeae
	2. Rosmarineae		2. Melitteae		a. Prunellinae
	3. Hormineae		3. Marrubieae		b. Melittinae
IV	Satureineae		4. Lamieae		c. Laminae
	1. Origaneae	VI	Prasieae		5. Glechoneae
	2. Hyssopeae	VII	Prostanthereae		6. Salvieae
	3. Cunileae	VII	Ajugeae		7. Meriandreae
V	Mellisinae				8. Monardeae
VI	Scutellarineae				9. Hormineae
VII	Prostanthereae				10. Lepechinieae
VIII	Nepeteae				11. Satureieae
IX	Stachydeae				a. Melissinae
	1. Melitteae				b. Hyssopinae
	1. Lamieae				c. Thyminae
	3. Marrubieae				d. Menthinae
	4. Balloteae				e. Perillinae
X	Prasieae				12. Pogostemoneae
XI	Ajugoideae			VII	Ocimoideae
					a. Hyptidinae
					b. Plectranthinae
					c. Moschosminae
				VII	Catopherioideae

difference between the classifications is one of rank, Briquet's divisions generally being made at one rank higher than those of the other authors.

Although some authors (e.g. Erdtman, 1945; El-Gazzar & Watson, 1970) have expressed dissatisfaction with Briquet's classification, it is accepted by most modern authors (e.g. Keng, 1969) as being superior to those of earlier workers. Briquet regarded the Pogostemoneae as a tribe characterized particularly by the 4–5 lobed corolla being equal or weakly bilabiate, and the anther locules showing some degree of fusion, and this concept of the group is followed here. A brief synopsis of the nomenclature is given below.

Tribe Pogostemoneae (Benth. ex Endl.) Briq. in Engl. & Prantl, *Natürl. Pflanzenfam.* **4** (3a): 326 (1897).
Tribe Menthoideae subtribe Pogostemeae Benth. ex Endl., *Gen. pl.*: 612 (1838).
Tribe Menthoideae subtribe Elsholtzieae Benth. ex Endl., *Gen. pl.*: 612 (1838).
Tribe Menthoideae subtribe Mentheae Benth. ex Endl., *Gen. pl.* : 612 (1838) *pro parte quoad Colebrookia sphalm.*
Tribe Satureieae subtribe Elsholtzieae Benth. in DC., *Prodr.* **12** : 149 (1848).
Tribe Satureieae subtribe Pogostemoneae Benth. & Hook.f., *Gen. pl.* **2** (2) : 1162, 1164 (1876).
Tribe Satureieae subtribe Menthoideae Benth. & Hook.f., *Gen. pl.* **2** (2) : 1162, 1164 (1876) *pro parte quoad Elsholtzia et Keiskea.*
Tribe Satureieae subtribe Pogostemoninae Kudo in *Mem. Fac. Sci. Agric. Taihoku imp. Univ.* **2** (2) : 45 (1929).

Previous taxonomic treatments of the Pogostemoneae

The Labiatae tribe Pogostemoneae comprises some 10 currently recognized genera, of which only three, *Dysophylla, Elsholtzia,* and *Pogostemon,* contain more than a dozen species. The taxonomic affinities of the genera within the Pogostemoneae and in related tribes have been subject to a number of different assessments and interpretations. The early literature in particular is fragmentary and confused. Few authors agree on the importance that should be attached to the various characters, or indeed which characters should be used in the consideration of the affinities and subsequent groupings. The results are at variance with each other and provide no clear picture as to the internal groupings of the tribe. The following account attempts to trace the history of the genera of the Pogostemoneae.

The first currently recognized genus, *Dysophylla* Blume, had earlier been given the polynomial *Veronica hirsuta latifolia Zeylanica aquatica* by Hermann (1717). Linnaeus (1747) used the generic name *Alopecuro–Veronica.* Later he (1767) described *M. auricularia* L., a plant of remote affinity to the other species of *Mentha*; here he placed in synonymy the names *Alopecuro–Veronica* and *Majorana foetida* (a plant described by Rumphius, 1750, as *Majana foetida*).

When Blume (1826) separated *Dysophylla* as a distinct genus based on *Mentha auricularia* he related it to, and placed it next to *Mentha* L., but considered it to differ by the closure of the fruiting calyx, the fleshy swelling of the disc and the distinctly bearded stamens. Under the only species, *Dysophylla auricularia* (L.) Blume, he cited Rumphius's illustration.

Willdenow (1790) described a new genus, *Elsholtzia*, based on a Silesian plant, *E. cristata* Willd. Although he gave a clear description and distinguished his genus from other Labiatae on corolla, calyx, stamen and inflorescence characters, a number of confused associations were made between this and other plants by later authors. Lamarck (1789) described five species in *Hyssopus* L., but his rather vague limits of the genus allowed for inclusion of two species of *Elsholtzia*, one of which was Willdenow's type species. Persoon (1806) amended Willdenow's genus description to add '*Flor. secundi, bracteati*' and described two new species, *E. paniculata* (referable to *Pogostemon*) and *E. ocymoides*. Don (1825) considered *Elsholtzia* congeneric with *Perilla* L. and reduced the name to synonymy. The description differed from that of *Perilla sensu* Linnaeus (1764) on a number of points but closely matched that of Willdenow's *Elsholtzia.*

Two new genera, *Leucosceptrum* and *Colebrookea,* were described by Smith (1805) based on

Nepalese specimens. *Leucosceptrum,* because of its habit, corolla and deeply lobed disc, was said to have affinities with the Verbenaceae, and because of the four-lobed corolla, exserted stamens and bilocular anthers, was considered close to *Mentha.* Smith described the corolla as having four unequal segments, the upper deeply emarginate, the lower large and entire. However, his illustration incorrectly shows the opposite of this, the lower segment being emarginate and the upper entire. The second monotypic genus, *Colebrookea,* was chiefly characterized by its fruit morphology. The distinctive hairy calyx with its plumose teeth acts as a pappus for the single-seeded, dry fruit. Roxburgh (1815) published an account of a second species of *Colebrookea, C. ternifolia* Roxb., based on plants collected in Mysore. All later authors, however, regard this merely as a variety of *C. oppositifolia,* leaving *Colebrookea* a monotypic genus. *C. oppositifolia* is a shrub and seems very different from the herbaceous species of *Elsholtzia.* In fact they do share a number of floral characters. Poiret (1817) produced a rather confusing situation when he published a new generic name *Elshotzia,* and put into it *Colebrookea oppositifolia* as a new combination. He even added the comment in the text 'ce genre est le mème que le *Colebrookea* de Smith. Il fait y rèunir le *barbula* de Loureiro'. The *'barbula'* of Loureiro (1790) is an earlier name for *Caryopteris* Bunge (Verbenaceae), which is strikingly similar to the Pogostemoneae in calyx, corolla, and anther characters.

Desfontaines (1815) described a new genus, *Pogostemon,* for a species with bearded stamens, *P. plectranthoides* Desf. (now = *P. benghalensis* (Burm. f.) Kuntze). Citing the shared similarity of calyx and corolla characters of *Pogostemon* and *Hyssopus* he claimed an affinity for his new genus; 'Le genre *Pogostemon* a de l'affinité avec l'Hyssope. La corolle renversée, les trois lobes de la levre supérieure entière et arrondis au sommet, les filets des étamines abaissés et barbus, sont les principaux charactères qui le distinguent'. Blume (1826) followed Desfontaines' description and published a second species from Java, *P. menthoides,* but which had naked filaments.

The first comprehensive review of all genera was Bentham (1829). He considered the original descriptions of *Dysophylla* and *Pogostemon* unsatisfactory and suggested modifications for both. In *Dysophylla* he placed less emphasis on the connivence of the calyx teeth, since it is a feature not common to all species. In *Pogostemon* he regarded the declination of the stamens to be so slight as to be of little significance, and he questioned Blume's inclusion of *P. menthoides,* since it appeared anomalous with the absence of hairs on the stamens, hairy stamens being a constant feature of all the other species of both genera. The delimitation of *Dysophylla* was expanded by Bentham to include those species of *Mentha* described by Loureiro (1790) and Roxburgh (1814, 1832).

Bentham reduced *Elsholtzia* to only one species, *E. cristata.* He created three new genera, all closely related to *Elsholtzia*: *Aphanochilus,* very similar to *Elsholtzia,* but differing in the exserted stamens with anther-locules confluent, the shrubby habit and non-secund inflorescence (the *Perilla* species described by Don (1825), although unknown to Bentham, belonged to *Aphanochilus*), the monotypic *Cyclostegia*, easily distinguished by its densely strobilate inflorescence, and *Tetradenia*, a Madagascan genus based on a plant labelled *Mentha fruticosa* in Hooker's herbarium; this differs from the other two genera in the irregular calyx and bright red, glandular swellings around the nutlets from which it is named.

A year later Bentham (1830) wrote a second account of the Labiatae. The only change from the earlier work was for *Dysophylla,* where he divided the genus for two parts on the basis of phyllotaxy. The first was characterized by opposite, paired leaves, and agreed with Blume's original description; it contained three species, *D. auricularia, D. myosuroides* Benth., and *D. strigosa* Benth. The second contained all *Dysophylla* species with verticillate leaves.

The first complete treatment of the Labiatae was by Bentham (1832–1836) in which he repeated his earlier descriptions for most of the genera and formally recognized his own divisions of *Dysophylla* (1830) as sections *Oppositifoliae* and *Verticillatae.* On the basis of inflorescence characters he divided *Pogostemon* into § *Paniculatae* and § *Racemosae. Aphanochilus* Benth. and *Cyclostegia* Benth., however, were reduced to sections of *Elsholtzia,* the distinctions being based primarily on morphological differences of the inflorescence and bracts.

Bentham considered *Leucosceptrum* to be a section of the unrelated genus *Teucrium* L. in his tribe Ajugoideae, which it resembled in lacking the upper lip of the corolla, in the hairiness of its fruits, and in its semi-shrubby habit.

Bentham's division of *Dysophylla* into sections *Oppositifoliae* and *Verticillatae* was taken further by Rafinesque-Schmaltz (1847) who published the genus *Eusteralis* based on *Mentha pumila* Graham and *M. verticillata* Roxburgh, which effectively raised section *Verticillatae* to generic rank. The problems posed by *Dysophylla* were also reflected by Hasskårl (1842), Miquel (1859), and Kuntze (1891), who were unable to distinguish it adequately from *Pogostemon* and included it as a section of that genus.

Miquel (1865) described four new species of *Elsholtzia,* three of which he referred to Bentham's section *Cyclostegia.* Bentham (in Bentham & Hooker, 1876) referred them to *Pogostemon* (see Hooker, 1896). This arrangement was based on the similarity of the anther structure, the anthers being subglobose, imperfectly two-celled and two-valved, as in *Pogostemon,* and not ovoid, distantly two-celled with the cells two-valved, as in *Elsholtzia.* One year later S. Moore (1877) removed Miquel's four species of *Elsholtzia* and placed them in the new genus *Comanthosphace.* Moore's view was that *Comanthosphace* approached *Elsholtzia* more nearly than *Pogostemon,* particularly in the two-lipped, five-lobed form of the corolla. This arrangement was fairly reliable, but Moore mistakenly described the verticillasters as being obscurely bracteate, an error pointed out by Hooker (1896). In fact the bracts are very large, another feature in common with *Elsholtzia,* but often caducous.

In the same paper, Miquel (1865) proposed a new genus, *Keiskea,* to accommodate material collected in Japan. When considering its affinities he gave its position as close to *Mentha,* although the description suggested closer affinities to *Elsholtzia* in that the corolla was sub-bilabiate with an emarginate upper lip and three-lobed lower lip. The filaments were hairy at the base, forming an incomplete annulus. Miquel described one species, *Keiskea japonica,* and the genus remained monotypic until Diels (1924) described a second species from China, *K. sinensis.* A third species, *K. elsholtzioides,* was described by Merrill (1937). He had difficulty in determining the affinities of this species and commented: 'In making the preliminary examinations this was placed in *Comanthosphace* from which its calyx characters exclude it. In its characteristic persistent, broad bracts it resembles *Elsholtzia* but in spite of these, seems to belong in *Keiskea.*' *K. elsholtzioides* Merrill differs markedly from the two previously known species of *Keiskea* which have narrower bracts and broadly campanulate calyces. Masamune (1940) described a Formosan species of *Keiskea, K. macrobracteata.* The conspicuous characters, bilabiate calyx and broadly ovate bracts, which distinguish it from *K. japonica* Miq. and *K. sinensis* Diels, prompted him to propose dividing the genus into two sections, *Macrobracteatae* and *Eukeiskea.*

The next major work on the Labiatae after Bentham was by Briquet (1897) although his account of the Pogostemoneae had no major changes from that of Bentham (1832–36). However, he described new subgeneric groupings in three genera. In *Pogostemon* he divided § *Racemosae* Benth. into: A. *Glabriuscula* with naked filaments and B. *Barbata* with hairy filaments. § *Paniculatae* Benth. was also divided into two groups designated only as A and B and distinguished by the density of the verticillasters (see Table 13). *Dysophylla* was divided into two sections: section *Goniocalicinae,* with strongly five-angled calyces, and section *Rhabdocalicinae,* with cylindrical calyces. Section *Rhabdocalicinae* was further divided by annual or perennial habit (see Table 14). Two new series were described in *Elsholtzia* section *Aphanochilus* : series *Platyelasmeae* Briq. (containing only *E. densa* Benth. and *E. eriostachya* (Benth.) Benth. and distinguished by broad bracts and matt nutlets) and series *Stenelasmeae* Briq. (containing the remaining species and distinguished by narrow bracts and shiny nutlets).

Another *Elsholtzia* species of dubious position was described by Rehder (1917) as *E. dependens.* 'This species seems not closely related to any other species of the genus. According to its broadly bracted spikes it ought to be placed in the group *Platyelasmeae* Briquet of the section *Aphanochilus* Bentham, but it differs from the species of this group as from those of the other groups in the entire upper lip of the corolla, in the irregular ring of hairs at the mouth of the corolla formed by hairy disc-like excrescences at the base of the filaments and in a hairy crescent-shaped crest below the base of the lower lip, and in the rostrate nutlets. The drooping habit of the long and slender spikes is also very peculiar and, so far as I know, does not occur in any other Elsholtzia.' Rehder's views were supported by Kudo (1929) in his monograph of the Chinese Labiatae. However, he took it one stage further and removed it from *Elsholtzia* and established a new, monotypic genus, *Rostrinucula*.

Kudo also revived Bentham's *Aphanochilus,* considering it to merit generic rank. This was not wholly accepted by other authors since many considered *Aphanochilus* and *Elsholtzia* to be congeneric, the calyx, anther, and bract characters being unreliable for separating the two.

During the last 50 years, very few major systematic changes have been made within the Pogostemoneae. Kitamura & Murata (1962) proposed the union of *Comanthosphace* and *Leucosceptrum*, citing the shape of both calyx and corolla, exsertion of stamens, anther shape, aerole size, and presence of stellate hairs on the leaves, as shared characters. As the authors did not examine all the species of either genus their views have not been generally accepted.

El-Gazzar & Watson (1967) made a study of *Dysophylla* and *Pogostemon*, using leaf characters, presence or absence of crystals in the calyx, and presence or absence of stem aerenchyma. They concluded that Bentham's *Dysophylla* section *Oppositifoliae* (containing four species, *D. auricularia, D. myosuroides, D. rugosa* Hook. f., and *D. salicifolia* Dalz, ex Hook. f.) should be sunk into *Pogostemon* since it shared the characters of opposite, broad, petiolate leaves, crystals present in the calyx, and stem-aerenchyma absent. *Dysophylla* section *Verticillatae* (containing all other *Dysophylla* species) was characterized by verticillate, linear, glabrous, sessile leaves, crystals absent from the calyx, and stem-aerenchyma present. Wu & Li (1975) also placed *D. auricularia* and *D. falcata* Wu in *Pogostemon* although they did not specify their reasons for so doing. These transfers of *Dysophylla* species, including the type species *D. auricularia*, to *Pogostemon* raised a nomenclatural problem for which a number of solutions were proposed and subsequently rejected. The latest and most satisfactory proposal, suggested by Bakhuizen van den Brink & van Steenis (1968), and also made by Panigrahi (1976), was to revive the name *Eusteralis* Rafin. for *Dysophylla* section *Verticillatae.* Keng (1978), however, combined *Dysophylla* and *Pogostemon* as congeneric taxa, and placed *Dysophylla* section *Verticillatae* in *Pogostemon* section *Eusteralis*.

Wu & Huang in their precursor account for the *Flora Reipublicae Popularis Sinicae* (1974), and later in the flora itself (1977), gave a generic account of the Chinese species of *Elsholtzia*. This covered 33 species and produced two new subsections and eight new series.

3. Methods

Reconstitution of material

All materials used in this study were obtained from herbarium specimens. Flowers and fruiting calyces were too brittle to be dissected without prior softening. The material was soaked in 4% sodium-orthophosphate solution for 12 hours, washed in distilled water, and stored in absolute alcohol.

Data compilation

The number of species and bulk of material available precluded the recording of every specimen for computation. Nevertheless, all available species were included in the sampling and all material was examined. To obtain full data for species (OTUs), three typical specimens were selected for scoring (Appendix 1) as a basis for each operational taxonomic unit. The species, their OTU numbers and acronyms are given in Table 2. The data were then averaged to produce single character statements for each species. Obscure or poorly understood taxa were scored wherever possible from authentic specimens.

Data on pollen were obtained from the literature except for *Eurysolen gracilis* Prain and *Leucosceptrum canum* Smith. Pollen samples from these two species were acetolysed and examined by light microscopy.

Table 2 The OTUs used in the analyses.

EGRA	1.	*Eurysolen gracilis*
EJAP	2.	*'Elsholtzia japonica'*
EFED	3.	*feddei*
EELE	4.	*'elegans'*
EPSE	5.	*pseudocristata*
ENIP	6.	*nipponica*
EOLD	7.	*oldhamii*
ECON	8.	*concinna*
ECIL	9.	*ciliata*
EKAC	10.	*kachinensis*
EPYG	11.	*pygmaea*
ESOU	12.	*soulei*
EARG	13.	*argyi*
ELUT	14.	*luteola*
EBOD	15.	*bodinieri*
EHET	16.	*heterophylla*
ESTR	17.	*strobilifera*
EHUN	18.	*hunanensis*
EERI	19.	*eriostachya*
EDEN	20.	*densa*
EMAN	21.	*manshurica*
EAQU	22.	*aquatica*
EINT	23.	*integrifolia*
EBED	24.	*beddomei*
EPEN	25.	*penduliflora*
ERUG	26.	*rugulosa*
ESTA	27.	*stauntonii*
EFLA	28.	*flava*
EFRU	29.	*fruticosa*
EPUB	30.	*pubescens*
ECOM	31.	*communis*
EALO	32.	*alopecuroides*
EGRI	33.	*griffithii*
EGLA	34.	*'glanduligera'*
EELA	35.	*elata*
EWIN	36.	*winitiana*
ESTC	37.	*stachyodea*
EBLA	38.	*blanda*
EMYO	39.	*myosurus*
EOCH	40.	*ochroleuca*
EPIL	41.	*pilosa*
ECAP	42.	*capituligera*
DTRI	43.	*'Dysophylla trinervis'*
DHEL	44.	*helferi*
DTOM	45.	*tomentosa*
DPEN	46.	*pentagona*
DSTO	47.	*stocksii*
DSAM	48.	*sampsonii*
DPEG	49.	*peguana*
DGRI	50.	*griffithii*
DYAT	51.	*yatabeana*
DCRA	52.	*crassicaulis*
DSTE	53.	*stellata*
DLIN	54.	*linearis*
DCRU	55.	*cruciata*
DQUA	56.	*quadrifolia*
DTSI	57.	*tsiangii*
DFAL	58.	*falcata*
DSZE	59.	*szemacensis*
DFAU	60.	*faurei*
DKOE	61.	*koehneana*
DGRA	62.	*gracilis*
DLYT	63.	*lythroides*
DPUM	64.	*pumila*
DMAI	65.	*mairei*
DAND	66.	*andersonii*
DGLA	67.	*'glabrata'*
DAUR	68.	*auricularia*
DSAL	69.	*salicifolia*
DRUG	70.	*rugosa*
DMYO	71.	*myosuroides*
PBEN	72.	*Pogostemon benghalensis*
PPAR	73.	*parviflorus*
PPAN	74.	*paniculatus*
PTUB	75.	*tuberculosus*
PGLA	76.	*glaber*
PHEY	77.	*heynianus*
PCAB	78.	*cablin*
PELS	79.	*elsholtzioides*
PAMA	80.	*amarantoides*
PFOR	81.	*formosanus*
PMEN	82.	*menthoides*
PFRA	83.	*fraternus*
PBRA	84.	*brachystachyus*
PMIC	85.	*micangensis*
PMUT	86.	*mutamba*
PNIG	87.	*nigrescens*
PPHI	88.	*phillipensis*
PREF	89.	*reflexus*
PRET	90.	*reticulatus*
PMOL	91.	*mollis*
PTRA	92.	*travancoricus*
PATR	93.	*atropurpureus*
PSPE	94.	*speciosus*
PVEL	95.	*velatus*
PWIL	96.	*williamsii*
PPUR	97.	*purpurascens*
PPAL	98.	*paludosus*
PVIL	99.	*villosus*
PWIG	100.	*wightii*
PROT	101.	*rotundatus*
PSTR	102.	*strigosus*
PHIS	103.	*hispidus*
PPUB	104.	*pubescens*
PBRE	105.	*brevicorollus*
PNEL	106.	*nelsonii*
PBAT	107.	*battakianus*
PWAT	108.	*wattii*
PHIR	109.	*hirsutus*
PRUP	110.	*rupestris*
PMAC	111.	*macgregorii*
PGAR	112.	*gardnerii*
PCHA	113.	*chaixii*
PDIE	114.	*dielsianus*

PGRI	115.	*griffiithii*
PNIL	116.	*nilagiricus*
PLIT	117.	*litigiosus*
RDEP	118.	*Rostrinucula dependens*
RSIN	119.	*sinensis*
CFOR	120.	*Comanthosphace formosana*
CSTE	121.	*stellipila*
CBAR	122.	*barbinervis*
CSUB	123.	*sublanceolata*
CJAP	124.	*japonica*
CNIN	125.	*ningpoensis*
CNAN	126.	*nanchuanensis*
LCAN	127.	*Leucosceptrum canum*
LPLE	128.	*plectranthoideum*
TGOU	129.	*Tetradenia goudotii*
THIL	130.	*hildebrandtii*
TFRU	131.	*fruticosa*
KJAP	132.	*Keiskea japonica*
KELS	133.	*elsholtzioides*
KGLA	134.	*glandulosa*
KSIN	135.	*sinensis*
KSZ	136.	*szechuanensis*
CTER	137.	*Colebrookea ternifolia*
COPP	138.	*oppositifolia*

Measurement of characters

The characters used in the study, their states and character type according to Gower's coefficient of similarity (Gower, 1971), are given in Table 3. Petiole length (character 2) was measured to the nearest millimetre. Bracteole and pedicel lengths (characters 15 and 64) were measured to the nearest 0·5 mm. The lengths of the longest and shortest calyx tooth, calyx tube at anthesis and in fruit, corolla tube and upper and lower corolla lips (characters 17, 18, 21, 22, 30, 32 and 33 respectively) were all measured to the nearest 0·05 mm. The number of leaves per whorl (character 4) was recorded only for those species with more than 2 leaves at a node (character 3). Wherever possible the leaves were counted from whorls in the middle of the stem. Characters 6, 7 and 8 refer to overall shape, basal shape, and apical shape respectively in the leaves. Each of the character states represents a broad class of shape: e.g., ovate. Each specimen was assigned to the most appropriate class and coded accordingly. A similar procedure was adopted with bract and bracteole shape (characters 11 and 14). The coded data for each OTU is given in Appendix 2. An asterisk denotes missing or non-applicable data.

Table 3 The characters scored, their states, and character types according to Gower's coefficient of similarity.

Characters	Type
1. Leaves : type 0 homophyllus 1 heterophyllus	1
2. Leaves : petiole length in millimetres	3
3. Leaves : phyllotaxis 0 opposite 1 verticillate	2
4. Leaves : number per whorl	3
5. Leaves : comparative size of members of a pair or whorl 0 equal 1 unequal	2
6. Leaves : shape 0 linear 1 ovate 2 orbicular 3 trifid	2
7. Leaves : basal shape 0 cuneate 1 attenuate 2 rounded 3 truncate	2
8. Leaves : apical shape 0 acute 1 acuminate 2 obtuse	2
9. Leaves : margin 0 entire 1 dentate 2 doubly dentate	2
10. Bracts : type 0 not membranous 1 membranous	2
11. Bracts : shape 0 linear 1 ovate 2 at least as broad as long	2
12. Bracts : fusion 0 free 1 connate for at least part of their length	2

Characters	Type
13. Bracts : persistence	2
0 persistent	
1 deciduous	
14. Bracteoles	2
0 absent	
1 linear	
2 lanceolate	
15. Bracteoles : length in tenths of a millimetre	3
16. Calyx : symmetry of teeth	2
0 regular	
1 irregular	
17. Calyx : length of longest tooth in hundredths of a millimetre	3
18. Calyx : length of shortest tooth in hundredths of a millimetre	3
19. Calyx : annulus in throat	2
0 absent	
1 present	
20. Calyx : number of main veins	3
21. Calyx : tube length at anthesis in hundredths of a millimetre	3
22. Calyx : tube length in fruit in hundredths of a millimetre	3
23. Calyx : tooth form in fruit	2
0 not plumose	
1 plumose	
24. Calyx : tooth position in fruit	2
0 incurved	
1 erect	
2 spreading	
25. Calyx : teeth hairs	2
0 absent	
1 present	
26. Calyx : tube hairs	2
0 absent	
1 present	
27. Calyx : angles	2
0 more or less terete	
1 strongly angled	
28. Corolla : symmetry	2
0 lower lip with 1 lobe	
1 lower lip with 2 lobes	
29. Corolla : division	2
0 upper lip not emarginate	
1 upper lip emarginate	
30. Corolla : tube length in hundredths of a millimetre	3
31. Corolla : exsertion	2
0 exserted	
1 not exserted	
32. Corolla : length of upper lip in hundredths of a millimetre	3
33. Corolla : length of lower lip in hundredths of a millimetre	3
34. Corolla : colour	2
0 not white	
1 white	
35. Corolla : colour	2
0 not yellow	
1 yellow	
36. Corolla : colour	2
0 not purple	
1 purple	
37. Corolla : annulus	2
0 absent	
1 complete ring of hairs	
2 interrupted ring of hairs	
38. Corolla : invagination	2
0 invagination absent	
1 invagination present	
39. Corolla : shape	2
0 corolla not gibbous above annulus	
1 corolla gibbous above annulus	
40. Stamens : exertion	2
0 exserted	
1 not exserted	
41. Anthers : size	2
0 all anthers equal	
1 lower pair reduced	
42. Filaments : length	2
0 equal	
1 lower pair longer	
2 upper pair longer	
43. Anthers : locule number	2
0 unilocular	
1 bilocular-fused	
2 bilocular-free	
44. Filaments : hairs	2
0 glabrous	
1 hairy towards base	
2 hairy towards middle	
45. Filaments : base	2
0 not bulbous	
1 bulbous	
46. Style : type	2
0 gynobasic	
1 terminal	
47. Style : lobes	2
0 plain	
1 clavate	
48. Style : basal shape	2
0 not bulbous	
1 bulbous	
49. Disc : number of tumescent glands	2
0 none	
1 one	
2 four	
50. Nutlets : hairs	2
0 absent	
1 present	
51. Nutlets : surface	2
0 not verrucose	
1 verrucose	

Characters	Type
52. Nutlets : apex	2
0 not rostrate	
1 rostrate	
53. Nutlets : number at maturity	2
0 one	
1 four	
54. Hairs : septate, eglandular	2
0 absent	
1 present	
55. Hairs : septate, glandular	2
0 absent	
1 present	
56. Hairs : branched, stalked	2
0 absent	
1 present	
57. Hairs : branched, sessile	2
0 absent	
1 present	
58. Indumentum : adaxial leaf surface	3
0 glabrous	
1 sparsely hairy	
2 densely hairy	
59. Indumentum : abaxial leaf surface	3
0 glabrous	
1 sparsely hairy	
2 densely hairy	
60. Indumentum : stem	3
0 glabrous	
1 sparsely hairy	
2 densely hairy	
61. Inflorescence : number of verticils per spike	3
62. Inflorescence : form of verticils	2
0 not secund	
1 sub-secund	
2 secund	
63. Inflorescence : number of flowers per verticil	3
64. Flowers : length of pedicel in tenths of a millimetre	3

The programs

The coded data were used to construct a similarity matrix using the measure of similarity described by Gower (1971). This matrix became the basis for analysis using the programs of the CLASP package (Rothamstead Experimental Station). This includes single-linkage and principal co-ordinates analyses (for full explanation see Gower, 1967 and Sneath & Sokal, 1973), a nearest neighbours list, and a method for clustering to maximize within-group mean similarity (WGMS). In this latter program all OTUs are randomly assigned to a preselected number of groups. An OTU is then transferred from one group to another if by doing so the WGMS is increased (and conversely the between-group mean similarity (BGMS) is decreased). This process is continued until further transfers no longer increase the WGMS. Since the number of groups is preselected, and every OTU must be assigned to a group, one may encounter the 'rag-bag' effect in which a number of unrelated OTUs are clustered to give a group with a very low WGMS.

4. Character variation

Most taxa in the Labiatae are very similar to each other in general appearance, and morphological variation tends to occur in relatively few characters. Characters which have long been considered of taxonomic importance (see Bentham, 1832–36, 1848; Endlicher, 1838; Bentham & Hooker, 1876; Briquet, 1897) within the Pogostemoneae include calyx and corolla shape, arrangement of stamens, and anther-locule number. A survey of 64 characters (see Table 3), and descriptions of variation within those which appear to be of taxonomic significance in the Pogostemoneae, is given below.

Leaves

All taxa have dorso-ventrally flattened leaves. Three basic lamina shapes are found; linear, ovate to orbicular, and lobed. The most common is the ovate to orbicular type, found in seven of the 10 genera (*Colebrookea*, Fig. 2, *Comanthosphace, Eurysolen*, Fig. 29, *Keiskea, Leucosceptrum, Rostrinucula*, Fig. 26, and *Tetradenia*). In addition most species of *Elsholtzia* (e.g. *E. ciliata*, Fig. 2) some species of *Pogostemon* (e.g. *P. mollis* Benth., Fig. 2) and *P. trinervis*

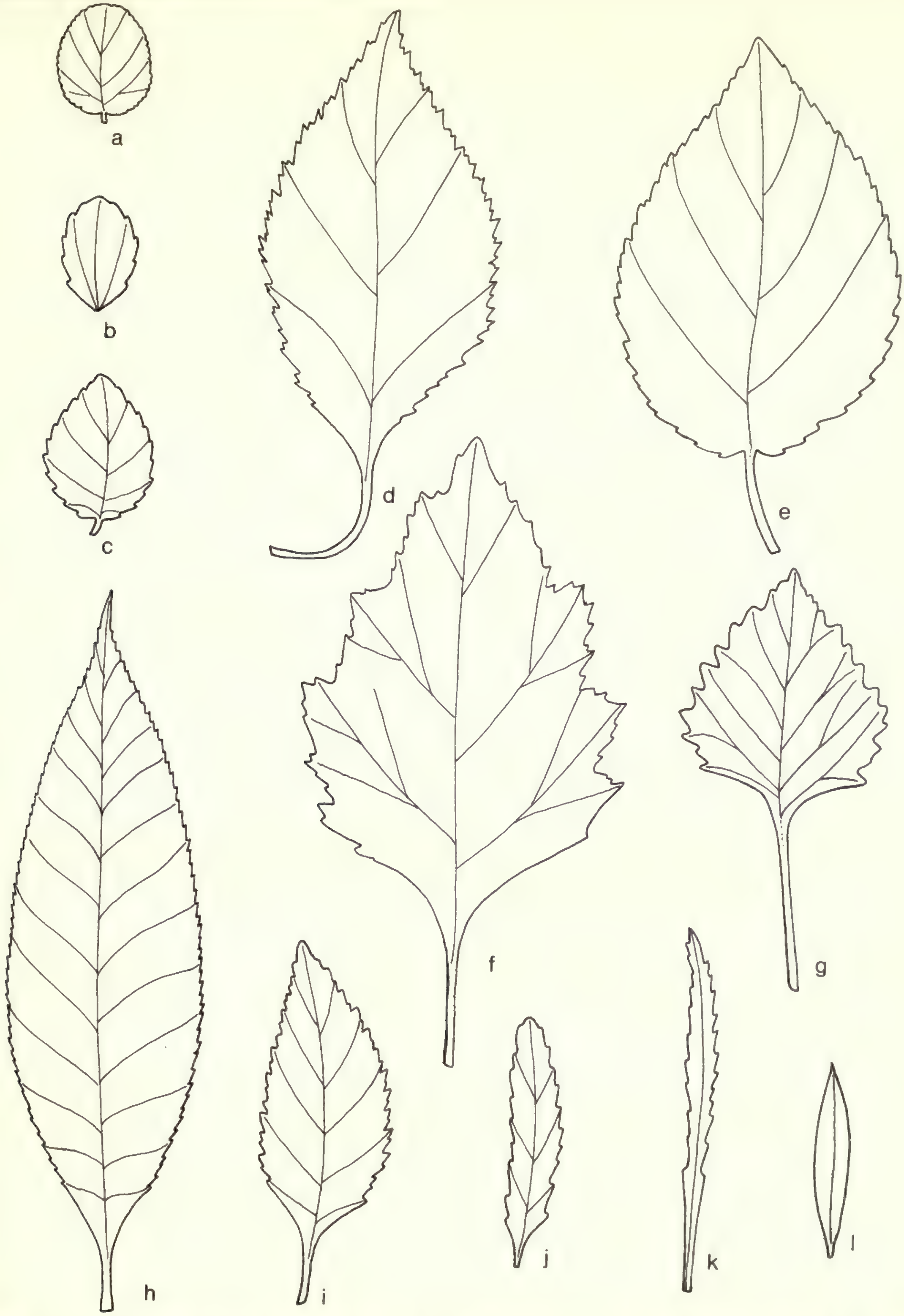

Fig. 2 Leaf shapes, margins, and petioles in the Pogostemoneae. (a) *Pogostemon mollis* × 1. (b) '*Dysophylla trinervis*' × 2. (c) *Elsholtzia kachinensis × 1. (d) Pogostemon glaber × 1. (e) Pogostemon speciosus* × 1. (f) *Pogostemon paniculatus* × 1. (g) *Elsholtzia stachyodea* × 1. (h) *Colebrookea oppositifolia* × 0.5. (i) *Elsholtzia ciliata* × 1. (j) *Elsholtzia densa* × 1. (k) *Dysophylla stellata* × 1. (l) *Dysophylla quadrifolia* × 1.

Chermsirivathana ex Press (see p. 74, Figs 2 & 33, provisionally called *'Dysophylla trinervis'* by Chermsirivathana, 1963) have leaves of this shape. The distinction between an ovate and an orbicular leaf is a fine one and the two characters tend to grade into each other. Linear leaves are found only in *Dysophylla* (see Fig. 2), *Pogostemon nilagiricus* Gamble, and *Elsholtzia pygmaea* W. Smith, although the latter is somewhat dubious since the observation is based on one specimen the leaves of which may better be considered as narrowly ovate. Three-lobed leaves occur in *Elsholtzia integrifolia* Benth.

Variation in the leaf apex shape is limited. Usually it is acute or acuminate, although obtuse apices are found in some species of *Dysophylla* (e.g. *'D. trinervis'*, Figs 2 & 33), *Elsholtzia* (e.g. *E. katchinensis* Prain, Fig. 2), *Pogostemon* (e.g. *P. mollis,* Fig. 2), and *Tetradenia* (e.g. *T. fruticosa* Benth.).

The leaf base shape can be divided into four character states; attenuate, cuneate, rounded, and tuncate. *Colebrookea* (Fig. 2), *Comanthosphace, Keiskea,* and *Rostrinucula* (Fig. 26) are exclusively cuneate. All *Tetradenia* species have rounded leaf bases. *Eurysolen gracilis* and *Leucosceptrum canum* (Fig. 29) have attenuate leaf bases. *Elsholtzia* and *Pogostemon* usually have cuneate (e.g. *E. heterophylla* Diels, Fig. 3, *P. glaber* Benth. in Wallich, Fig. 2), or attenuate (e.g. *E. stachyodea* (Link) Raiz & Saxena, Fig. 2) leaf bases, although a few species have rounded leaf bases (e.g. *E. kachinensis,* Fig. 2, *P. speciosus* Benth., Fig. 2). Truncate leaf bases are confined to *Dysophylla* (e.g. *D. stellata* (Lour.) Benth., Fig. 2) although *'D. trinervis'* (Figs 2 & 33) and *D. koehneana* Muschler in Fedde have cuneate leaf bases, and in *D. quadrifolia* (Roxb.) Benth. (Fig. 2) the leaf base is usually attenuate.

The leaf margins show varying degrees of incision, which may be conveniently scored as entire, dentate, or doubly dentate. *Colebrookea* (Fig. 2), *Comanthosphace, Keiskea, Rostrinucula* (Fig. 26), *Eurysolen gracilis* and *Leucosceptrum canum* (Fig. 29) all have dentate margins. In *Pogostemon* and *Tetradenia* the margin may be dentate (e.g. *Pogostemon mollis,* Fig. 2, *Tetradenia fruticosa*) or doubly dentate (e.g. *Pogostemon paniculatus* (Willd.) Benth., Fig. 2, *Tetradenia goudotii* Briq.). In *Dysophylla* the margins may be entire (e.g. *Dysophylla tomentosa* Dalz., Fig. 3) or dentate (e.g. *Dysophylla stellata,* Fig. 2). *Elsholtzia* exhibits the whole range from entire (e.g. *Elsholtzia integrifolia*) to dentate (e.g. *Elsholtzia densa* Figs 2 & 28) and doubly dentate (e.g. *Elsholtzia ciliata,* Fig. 2).

Heterophylly

Heterophylly is rare but is found in two species of *Elsholtzia* (*E. bodinieri* Vaniot and *E. heterophylla,* Fig. 3). Unlike most taxa these two species possess leaves on the stolons which are much smaller, usually broader, and much hairier than the cauline leaves.

Leaf size

The Labiatae normally have one pair of leaves at each node of the stem; each leaf of a pair is identical to the other. *Pogostemon gardneri* Hook. f. and *P. paniculatus* (Fig. 3) are unusual in having one leaf of a pair much smaller than the other. This feature is occasionally found in *P. purpurascens* Dalz., but is absent from the remainder of the Pogostemoneae.

Phyllotaxis

The Pogostemoneae (excluding *Dysophylla* section *Verticillatae*) usually follow the general Labiatae pattern of opposite, decussate leaf pairs, *Colebrookea ternifolia* is supposed by some authors to have ternate leaves but I have never found this. Species of *Dysophylla* section *Verticillatae* Benth. (Fig. 3) are very distinct in having whorls of leaves at each node. The number of leaves per whorl varies between, but is usually constant within each species; the most common numbers are three, four, and five, but *D. stocksii* Hook.f. may have 14 or more leaves per whorl.

Petioles

Petiole length is sometimes difficult to ascertain, especially in species with attenuate leaf bases, but when a distinct petiole is present it varies from 1 mm (e.g. *Elsholtzia heterophylla,* Fig. 3) to 80 mm (e.g. *E. fruticosa*) long. In most *Dysophylla* species the leaves are sessile, but *D. quadrifolia* (Fig. 2) and a few other species have short but quite distinct petioles.

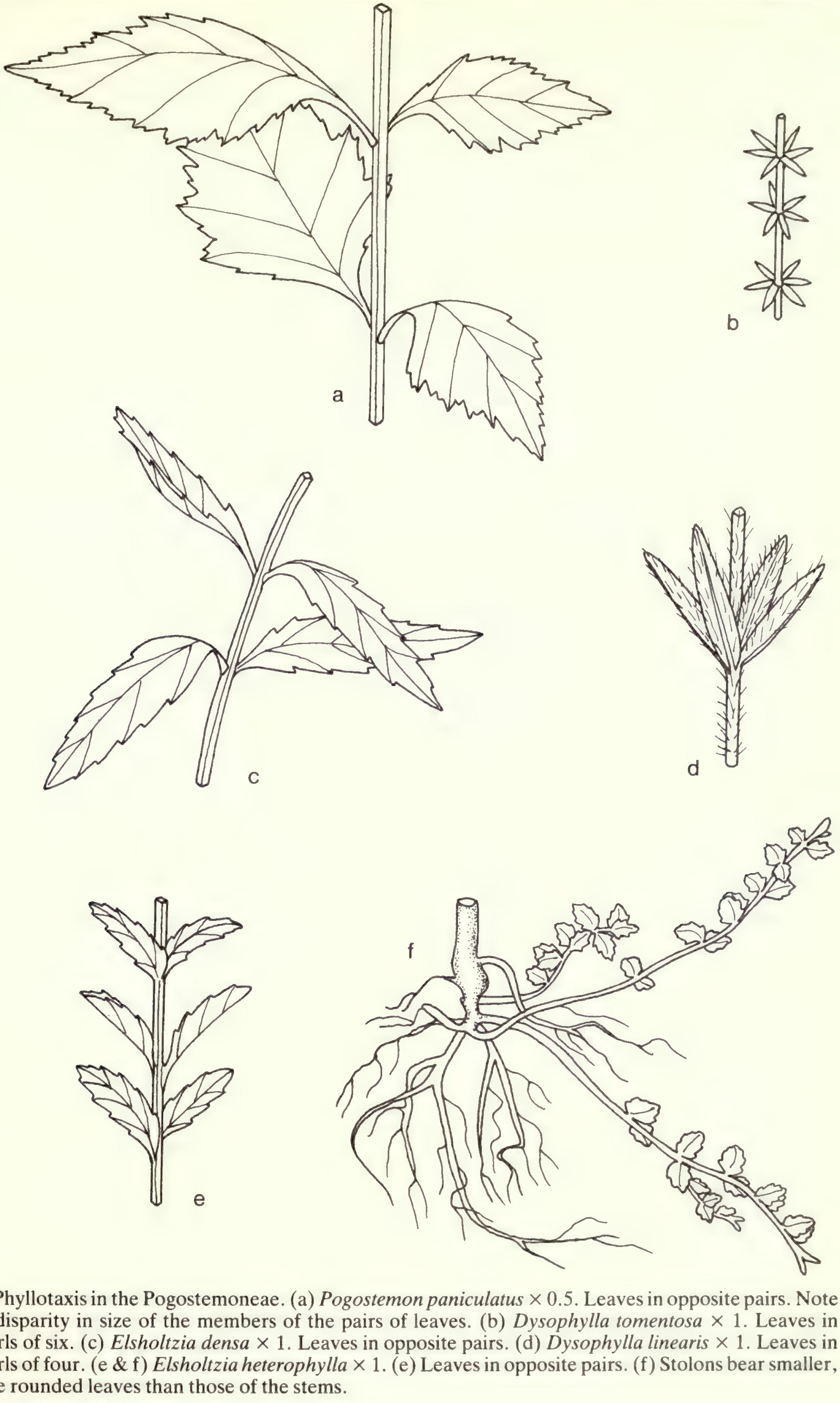

Fig. 3 Phyllotaxis in the Pogostemoneae. (a) *Pogostemon paniculatus* × 0.5. Leaves in opposite pairs. Note the disparity in size of the members of the pairs of leaves. (b) *Dysophylla tomentosa* × 1. Leaves in whorls of six. (c) *Elsholtzia densa* × 1. Leaves in opposite pairs. (d) *Dysophylla linearis* × 1. Leaves in whorls of four. (e & f) *Elsholtzia heterophylla* × 1. (e) Leaves in opposite pairs. (f) Stolons bear smaller, more rounded leaves than those of the stems.

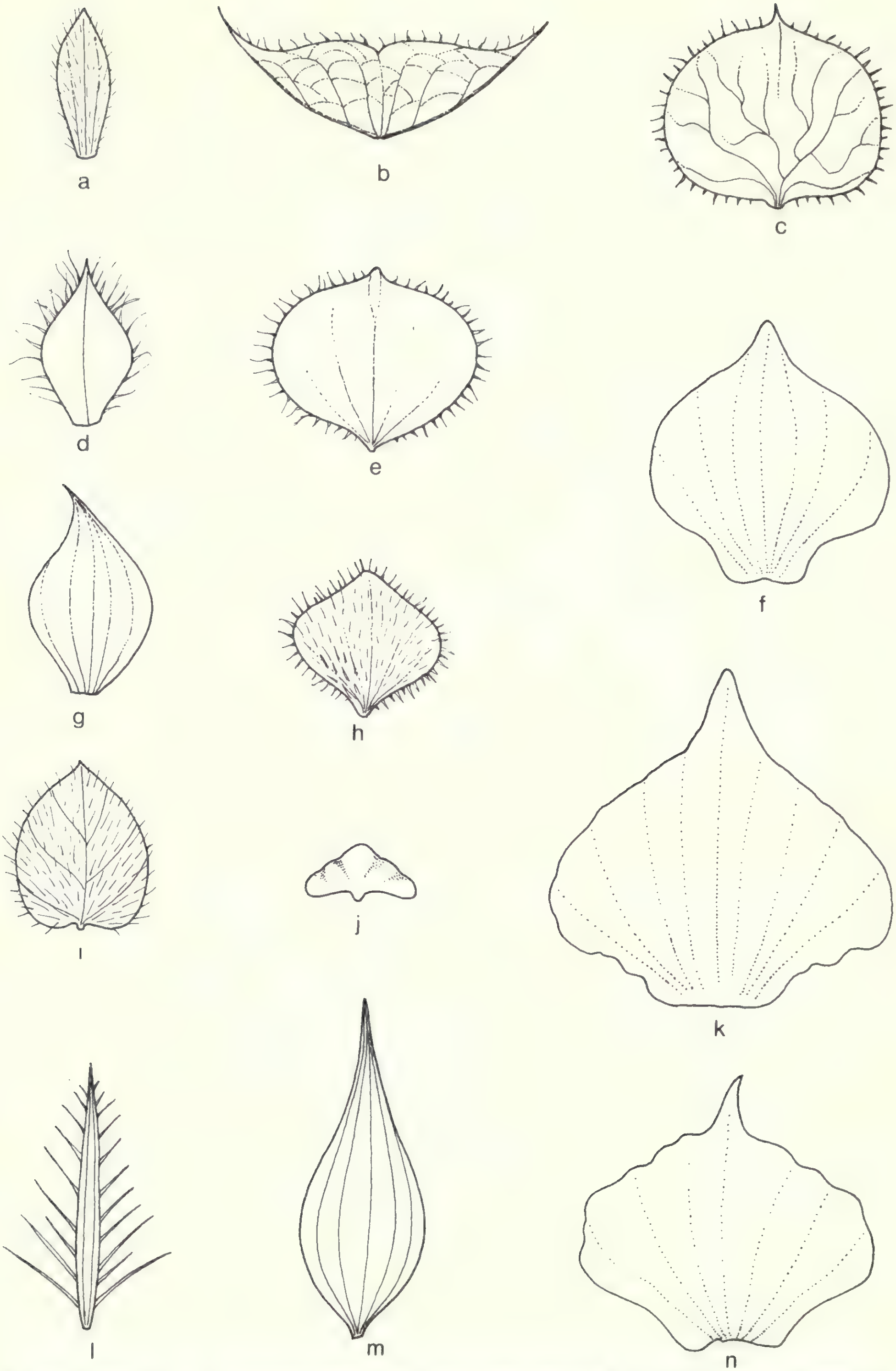

Fig. 4 Bract types in the Pogostemoneae. (a) *Eurysolen gracilis* × 5. (b) *Elsholtzia luteola* × 5. (c) *Elsholtzia ciliata* × 5. (d) *Dysophylla auricularia* × 10. (e) *Elsholtzia kachinensis* × 5. (f) *Rostrinucula dependens* × 5. (g) *Elsholtzia flava* × 5. (h) *Elsholtzia densa* × 5. (i) *Pogostemon paniculatus* × 5. (j) *Tetradenia fruticosa* × 10. (k) *Comanthosphace japonica* × 5. (l) *Elsholtzia pilosa* × 5. (m) *Keiskea elsholtzioides* × 5. (n) *Leucosceptrum canum* × 5.

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Bracts

The Pogostemoneae show considerable bract variation, particularly in colour, shape, fusion, and persistence. Six combinations of these four characters can occur:

(1) Bracts brown, broader than long, free, deciduous; this combination is found in *Comanthosphace, Rostrinucula* and *Leucosceptrum canum* (Figs 4, 26). The bracts often fall before the flower buds open.

(2) Bracts brown, broader than long, free, persistent; this combination is found in *Tetradenia* and *Elsholtzia* section *Elsholtzia* and *Elsholtzia* section *Aphanochilus* series *Platyelasmeae* (Figs 4, 28). In *Elsholtzia* section *Elsholtzia* the bracts are membranous.

(3) Bracts brown, broader than long, fused, persistent; in *Elsholtzia* section *Cyclostegia* and *E. luteola* Diels (Figs 4, 27) the bracts are again membranous and each pair is connate at the margins, forming a cyathium.

(4) Bracts green, broader than long, free, persistent; in *Elsholtzia concinna* Vaut. and *E. kachinensis* (Fig. 4) the bracts are green and never membranous.

(5) Bracts green, ovate, free, persistent; this type includes the following (all shown in Fig. 4): some *Dysophylla* species (e.g. *D. auricularia*), *Elsholtzia flava* (Benth.) Benth., *Eurysolen gracilis, Keiskea,* and some *Pogostemon* species (e.g. *P. paniculatus*).

(6) Bracts green, linear, free, persistent; *Colebrookea* and the remaining species of *Dysophylla* (e.g. *D. peguana* Prain), *Elsholtzia* (e.g. *E. pilosa* (Benth.) Benth. Fig. 5), and *Pogostemon* (e.g. *P. fraternus* Miq.) all have this character combination.

Bracteoles

Bracteoles may be present or absent. When present they are usually shorter, narrower, and more hairy than the bracts. Bracteoles are absent in *Keiskea, Tetradenia, Elsholtzia* sections *Elsholtzia* and *Cyclostegia*, and section *Aphanochilus* series *Platyelasmeae.* In *Comanthosphace, Rostrinucula,* and *Leucosceptrum canum* the bracteoles are caducous, and, like the bracts, often fall before the flower buds open.

Indumentum

Four hair types (Fig. 5) are found:

(1) Septate eglandular hairs; these are simple hairs each at least several cells long. The cells are laterally compressed and arranged so that the narrow sides alternate along the length of the hair, and the terminal cell is usually somewhat pointed.

(2) Septate glandular hairs; these are structurally identical with the septate eglandular hairs except for the terminal cell, which is a globular, single-celled gland.

(3) Branched stalked hairs; these are the 'stellate' hairs of earlier authors, each hair in fact having a central axis bearing irregular branches along its length. The hairs are multicellular, the septa clearly visible.

(4) Branched sessile hairs; similar to branched stalked hairs, but distinguished by the lack of a central axis, the branches radiating irregularly from a central point.

Most species have septate, eglandular hairs only. A number of species e.g. *Dysophylla linearis* Benth. and *Pogostemon brachystachyus* Benth. have a mixture of glandular and eglandular septate hairs. Branched stalked hairs are less common, being found in five genera. *Comanthosphace, Leucosceptrum,* and *Rostrinucula* bear branched stalked hairs with a few septate eglandular hairs. *Tetradenia* and a number of *Elsholtzia* species, e.g. *E. capituligera* (Dunn) Y. C. Wu and *E. stachyodea*, have a mixture of branched stalked and septate eglandular hairs. Other species, e.g. *E. eriostachya* and *E. fruticosa*, have branched stalked, septate eglandular and septate glandular hairs. Branched sessile hairs are found in two species of *Pogostemon*: in *P. tuberculosus* Benth. the hairs have a central boss from which the short stiff branches radiate, whilst in *P. velatus* Benth. there is no central boss and the branches are long and flexuous.

All species possess some hairs, although these may be restricted to the inflorescence. The abaxial leaf surface is always more hairy than the adaxial; the veins more hairy than the surface of the lamina. The density of hairs on the stems decreases with age, so that the lowest parts of the

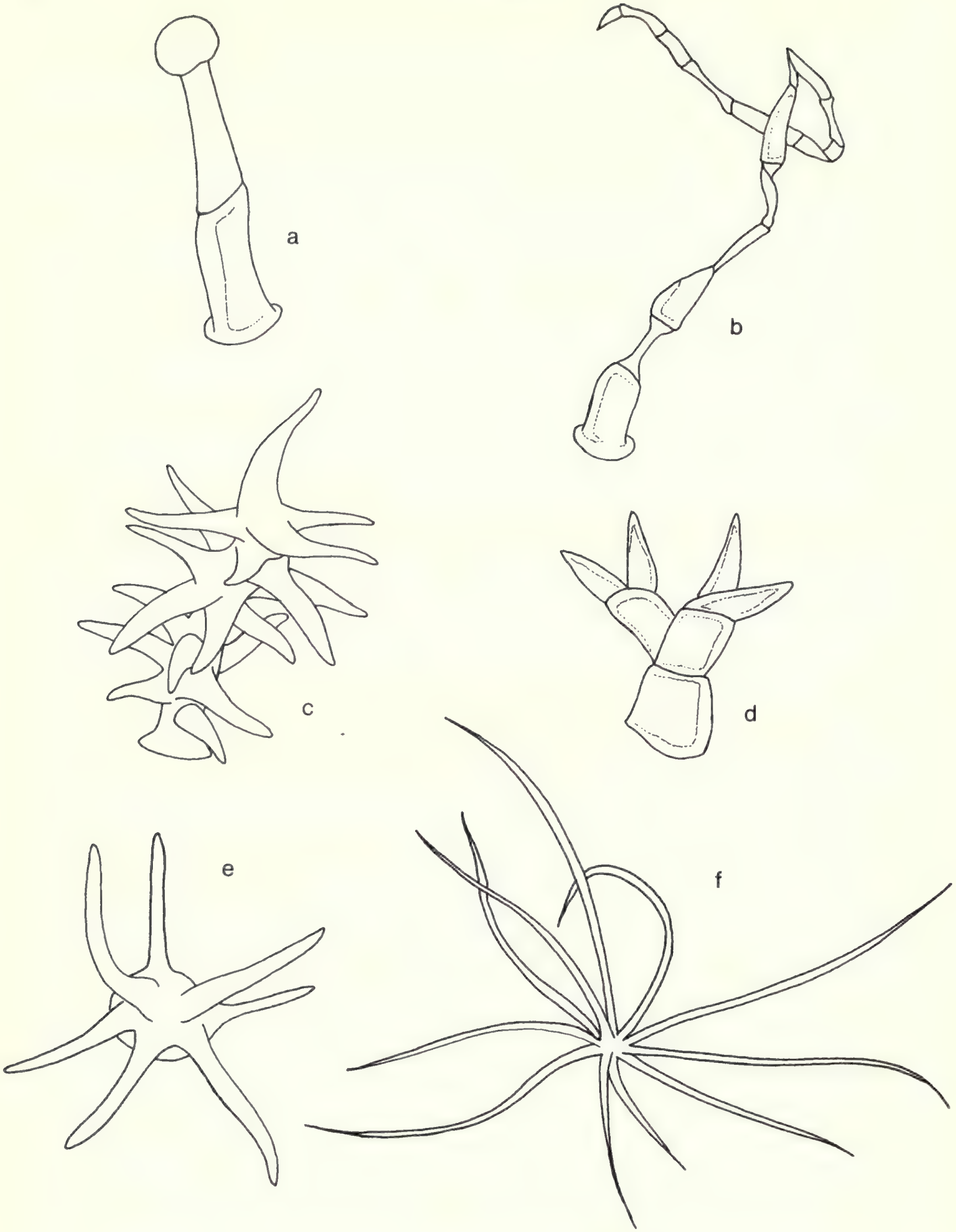


Fig. 5 Hair types in the Pogostemoneae. (a) septate glandular hair. (b) septate eglandular hair. (c & d) branched stalked hairs. (e) branched sessile hair, the branches short and stiff. (f) branched sessile hair, the branches long and flexuous.

stem are frequently glabrous. The density of the indumentum varies between individuals as well as between species.

Only *Pogostemon glaber* and some species of *Dysophylla,* e.g. *D. yatabeana* Makino, have glabrous stems and leaves. All other species have some indumentum here, ranging from very thin, e.g. *Elsholtzia luteola,* to very dense, e.g. *Pogostemon mollis.*

Calyx

The calyx is generally campanulate, five toothed, with the teeth sometimes much elongated. The teeth are unequal in *Keiskea* (Fig. 6), most *Elsholtzia* species (e.g. *E. ciliata,* Fig. 6 and *E. densa,* Figs 6, 28) and some species of *Pogostemon* (e.g. *P. fraternus,* Fig. 6). In *Tetradenia* (Fig. 6) the upper tooth is much the broadest and overlaps the lateral teeth.

The calyx tube is strongly veined, the most prominent veins generally considered as the main veins. Three species, *Comanthosphace ningpoensis* (Hemsley) Hand.-Mazz., *Elsholtzia integrifolia,* and '*Elsholtzia japonica*' have 15 main veins; *Comanthosphace* (excluding *C. ningpoensis*) and *Leucosceptrum canum* (Fig. 6) have 12. The remaining taxa have five or 10 main veins, although in some species of *Dysophylla* (e.g. *D. tomentosa*) the number is difficult to determine. The main, central veins of the teeth are thickened to form five strong ribs in *Colebrookea* (Fig. 6), *D. griffithii* Hook.f., *Dysophylla pentagona* C.B. Clarke ex Hook.f., and *D. stocksii.*

The calyx is usually hairy on the outer surface, and the teeth are fringed with cilia. Three species, *Elsholtzia kachinensis, E. penduliflora* W. Smith and *Pogostemon glabratus* Chermsirivathana ex Press (see p. 71, Fig. 32, provisionally called '*Dysophylla glabrata*' by Chermsirivathana, 1963) have a glabrous calyx. *Keiskea japonica* (Fig. 6) has a hairy calyx-tube but glabrous teeth, while several species, including *Pogostemon amarantoides* Benth. and *P. paludosus* Benth., have a glabrous calyx-tube and hairy teeth.

The presence of an annulus of stiff hairs in the throat of the calyx is confined to *Keiskea* and some species of *Pogostemon* (e.g. *P. fraternus* and *P. litigiosus* Doan, both in Fig. 6).

The calyx may be accrescent at the fruiting stage. In *Elsholtzia* series *Platyelasmeae* the increase in size is striking, the fruiting calyx (Figs 6, 28) being up to eight times larger than at anthesis. In *Colebrookea* the calyx teeth are plumose, becoming greatly elongated but not much widened in fruit.

The calyx teeth are normally erect during fruiting, but in *Dysophylla stellata* and *Pogostemon litigiosus* they are spreading and in other species of *Dysophylla* (e.g. *D. pentagona*) and *Pogostemon* (e.g. *P. nelsonii* Doan) strongly incurved.

Corolla

The corolla is zygomorphic, although in some species of *Dysophylla* weakly so and not obviously bilabiate. Generally the corolla lobes are arranged to form an upper group of three lobes and a single lower lobe. *Elsholtzia integrifolia* is exceptional in having a bifid lower lobe. In *Dysophylla, Pogostemon,* and *Rostrinucula* (Fig. 26) the upper central lobe is entire; in the remaining six genera it is shallowly to deeply emarginate.

The corolla tube shows little variation except in length. At maturity it may reach 9·5 mm in length (e.g. *Elsholtzia bodinieri*) or be as little as 0·5 mm long (e.g. *Tetradenia hildebrandtii* Briq.) and is usually rather slender at the base widening gradually to the throat. In *Pogostemon* the upper lip is longer than or equals the lower lip. In the other genera the lower lip is longer than or equals the upper lip.

An annulus of hairs is found in the corolla throat of six genera. In *Comanthosphace, Keiskea,* and *Tetradenia* (Fig. 7) the annulus is a complete ring at, or slightly below, the level of insertion of the staminal filaments. In a number of *Elsholtzia* species, e.g. *E. capituligera, E. hunanensis* Hand.-Mazz., and *E. stauntonii* Benth. (Fig. 7), the annulus is an open ring, the lines of hairs projecting dorsally and ending under the upper lip. *Rostrinucula* (Figs 7, 26) has a partial annulus composed of clusters of hairs at the insertion point of each staminal filament. In addition to the hair-clusters there is an invagination on the ventral surface of the corolla forming a crescent-shaped papilla in the throat, itself also hairy and forming part of the annulus.

In *Eurysolen gracilis* (Figs 7, 29) the corolla is gibbous slightly above the base. An invagina-

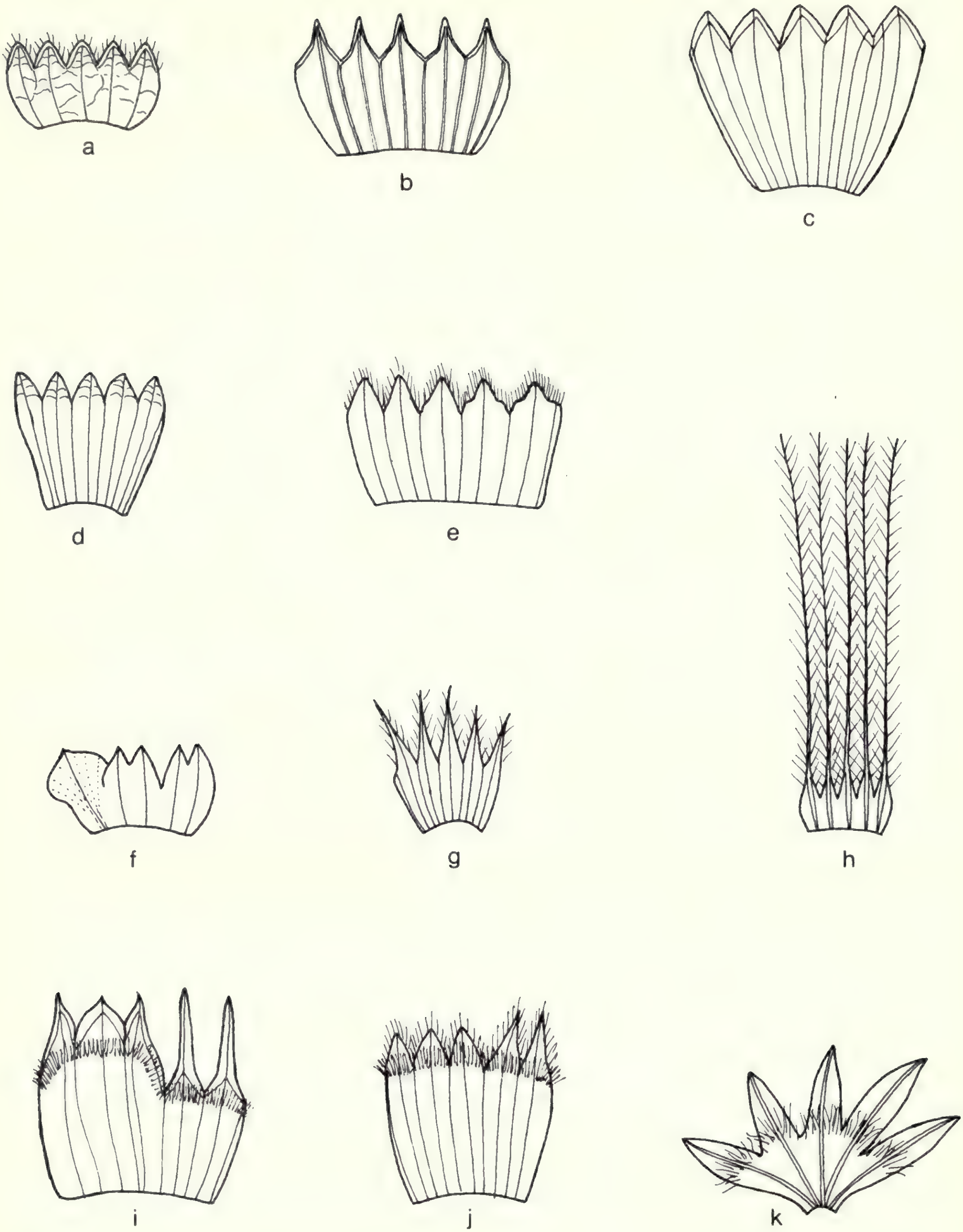


Fig. 6 Calyx shapes and veination in the Pogostemoneae. Only the main veins are shown. (a) *'Dysophylla trinervis'* × 5. (b) *Elsholtzia flava* × 5. (c) *Leucosceptrum canum* × 5. (d) *Pogostemon parviflorus* × 5. (e) *Elsholtzia densa* (fruiting) × 5. (f) *Colebrookea oppositifolia* (fruiting) × 10. (g) *Tetradenia goudotii* × 5. (h) *Elsholtzia ciliata* × 5. (i) *Pogostemon litigiosus* × 5. (j) *Pogostemon fraternus* × 5. (k) *Keiskea japonica* × 5.

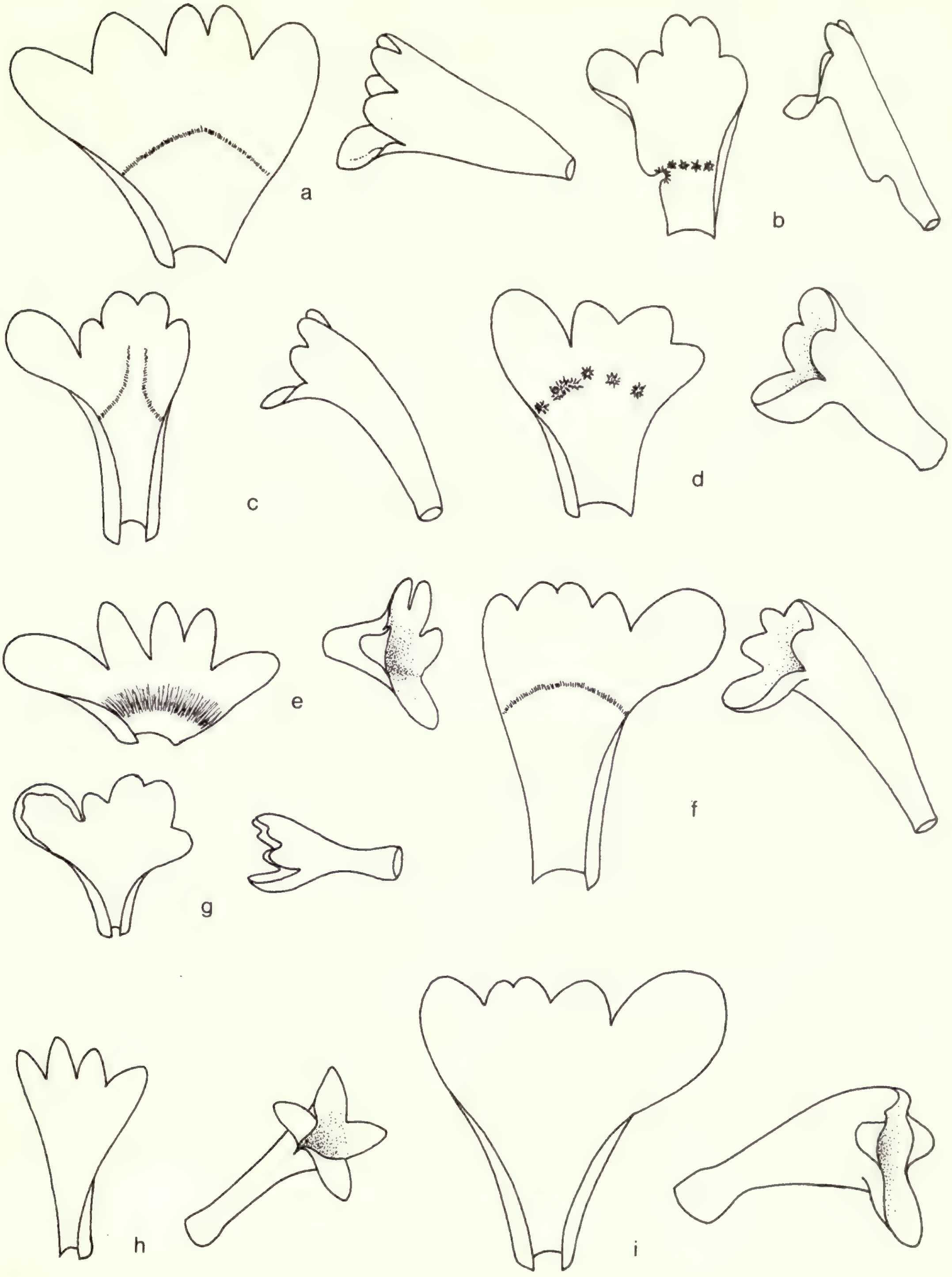


Fig. 7 Corolla structures in the Pogostemoneae. (a) *Keiskea japonica* × 5. (b) *Eurysolen gracilis* × 5. (c) *Elsholtzia stauntonii* × 5. (d) *Rostrinucula dependens* × 5. (e) *Tetradenia fruticosa* × 5. (f) *Comanthosphace japonica* × 5. (g) *Colebrookea oppositifolia* × 20. (h) *Pogostemon tuberculosus* × 5. (i) *Leucosceptrum canum* × 5.

tion similar to that in *Rostrinucula* occurs immediately below the gibbous curve forming a hairy papilla which all but closes the corolla tube.

The corollas are usually yellow, white, and rose-pink to purple, the latter being most common.

Stamens

In common with most Labiatae, the Pogostemoneae have four stamens arranged into two pairs: an upper and a lower pair. The filaments may be equal in length or one pair longer than the other. In *Colebrookea, Rostrinucula* (Fig. 26) and *Tetradenia* the filaments are equal; in *Eurysolen gracilis* (Fig. 29) the upper filaments are longest; in *Comanthosphace, Keiskea,* and *Leucosceptrum canum* the lower filaments are longest. In the remaining genera all three conditions can occur.

The anthers are almost always exserted, the only exceptions being *Elsholtzia aquatica* C.H. Wright and *Elsholtzia* series *Platyelasmeae* (Fig. 28).

The filaments are inserted towards the top of the corolla tube. In *Eurysolen gracilis* (Figs 26, 29), *Rostrinucula dependens* (Rehder) Kudo, and *R. sinensis* (Hemsley) Y.C. Wu, each filament is marked by a bulbous swelling below the point of insertion, which bears annular hairs.

Dysophylla, Pogostemon, and *Leucosceptrum canum* (Fig. 8) have hairs on the filaments. In the first two genera the hairs are long, thread-like, and usually purple due to cross-wall pigments. In *Leucosceptrum canum* the hairs are short and white. In *Dysophylla* and most species of *Pogostemon* the hairs are borne towards the middle of the filament; in *Leucosceptrum canum* (Fig. 8) and some species of *Pogostemon* (e.g. *P. hispidus* Prain and *P. travancoricus* Beddome, Fig. 8) the hairs are borne towards the base of the filament.

The anthers are usually equal in size. However *Elsholtzia pilosa* has two smaller, lower anthers often reduced to half the size of the upper ones.

Anthers are bilocular in *Elsholtzia, Keiskea* (Figs 8, 27, 28), and *Tetradenia* and unilocular in the remaining genera. *Tetradenia* and most species of *Elsholtzia* have locules confluent through partial fusion. *Keiskea, Elsholtzia hunanensis,* and '*E. japonica*' have distinctive free locules.

Style

Two style types occur in the Labiatae; (1) gynobasic, when the style arises from the base of, and between, the deeply-divided lobes of the ovary, (2) terminal, when the ovary is shallowly-lobed and the style is not basal. Gynobasic styles are found throughout the family except for the subfamily Ajugoideae which have terminal styles. In *Leucosceptrum canum* (Fig. 9) the style usually appears terminal but in some specimens it more nearly approaches the gynobasic condition. The reverse seems true of *Elsholtzia flava* (Fig. 9). All other Pogostemoneae have gynobasic styles.

The style is typically long, slender and straight or slightly curved, with a bifid tip. The lobes at the tip are subulate and equal. In *Elsholtzia* the style may vary in base and lobe shape. In some species (e.g. *E. ochroleuca* Dunn, *E. stachyodea*, Fig. 8) the style bears a bulbous swelling at the base, just above the point of emergence from between the nutlets. In *Elsholtzia* series *Platyelasmeae* (Fig. 8) the style lobe tips are clavate, a condition found also in *Pogostemon litigiosus*.

Disc

The disc may be regular or may bear one to several tumescent lobes. In *Elsholtzia* and *Keiskea* (Figs 8, 27, 28) there is a single, somewhat elongated lobe on the posterior edge of the disc. In *Tetradenia* (Fig. 8) there are four lobes, spaced regularly around the disc. They are bright-red and quite large, overtopping the young nutlets. The other genera have regular discs.

Nutlets

In the Labiatae there are usually four nutlets, a feature generally true of the Pogostemoneae. Exceptions are *Colebrookea oppositifolia* (Fig. 10), *Dysophylla stocksii*, *Esholtzia kachinensis*

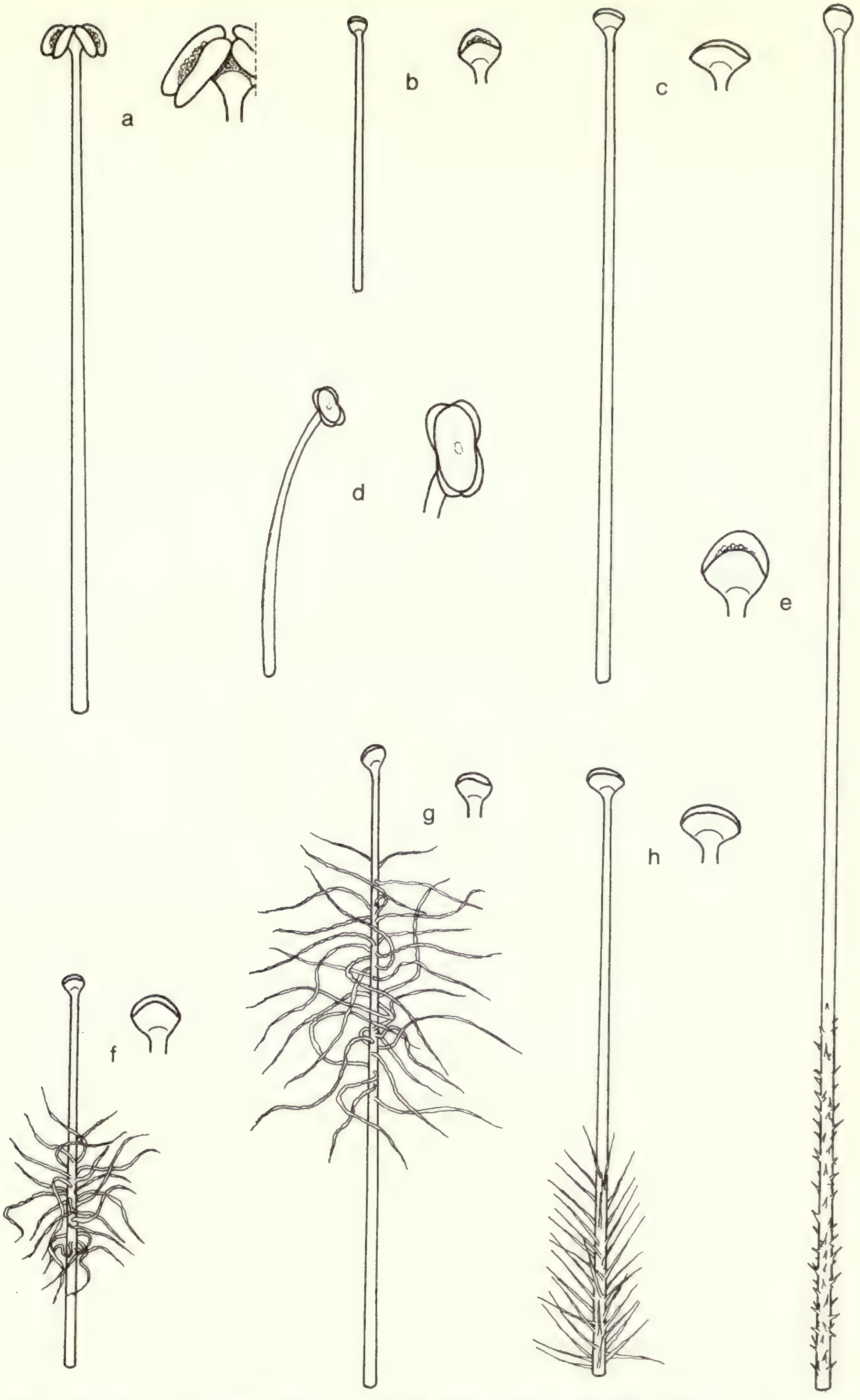


Fig. 8 Stamen types in the Pogostemoneae. All stamens × 10. All anther details × 20. (a) *Keiskea japonica*. (b) *Colebrookea oppositifolia*. (c) *Comanthosphace sublanceolata*. (d) *Elsholtzia ciliata*. (e) *Leucosceptrum canum*. (f) *Dysophylla linearis*. (g) *Pogostemon parviflorus*. (h) *Pogostemon atropurpureus*.

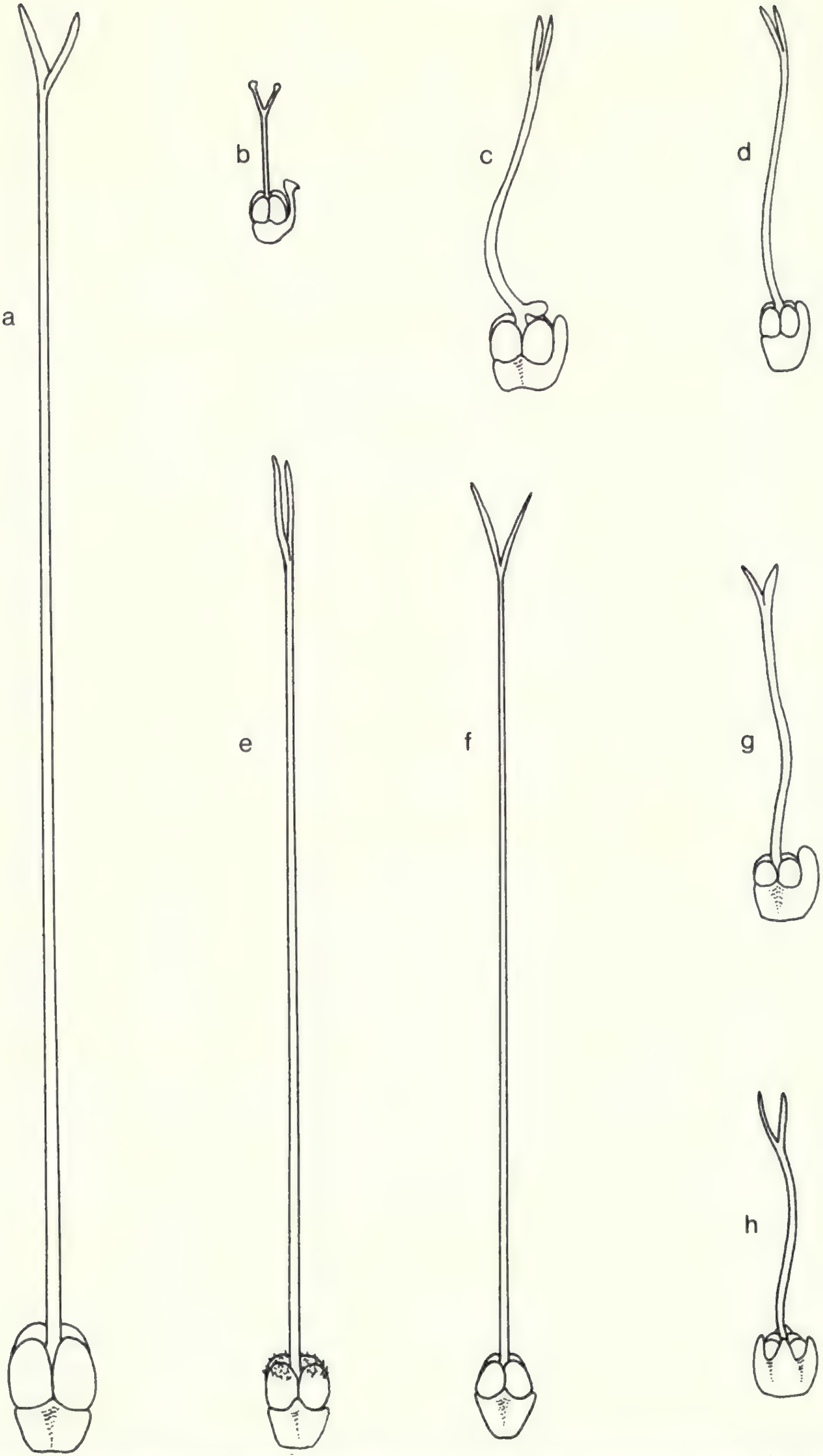


Fig. 9 Style and disc types in the Pogostemoneae. All × 10. (a) *Leucosceptrum canum*. (b) *Elsholtzia densa*. (c) *Elsholtzia stachyodea*. (d) *Elsholtzia fruticosa*. (e) *Comanthosphace japonica*. (f) *Pogostemon tuberculosus*. (g) *Keiskea japonica*. (h) *Tetradenia fruticosa*.

and *Keiskea japonica* (Fig. 10) with only one nutlet at maturity, the other three nutlets apparently undergoing early abortion.

The nutlets are generally obovoid and blunt at the apex. However, *Rostrinucula* nutlets (Figs 10, 26) have a rostrate tip at maturity.

Hairy nutlets are found in *Colebrookea* (Fig. 10), *Rostrinucula* (Figs 10, 26), all *Comanthosphace* species (Figs 9, 10) except *C. nanchuanensis* Y.C.Wu & Li, and in *Elsholtzia japonica* where the hairs are confined to the apex of the nutlet. All other species have glabrous nutlets.

Variation in nutlet ornamentation is limited. Most species have nutlets with a smooth to slightly rugulose surface. By contrast those of *Elsholtzia* series *Platyelasmeae* (Figs 10, 28) are distinctly verrucose towards the apex. In *Keiskea japonica* (Fig. 10) the nutlet has ridges which form an almost reticulate pattern.

In *Colebrookea* the single ripe nutlet does not separate from the calyx, the two structures acting as a single dispersal unit.

Inflorescence

The inflorescence is usually racemose (paniculate in some species of *Pogostemon*). It varies greatly in length, and in the number of whorls of flowers, or verticils. The verticils are secund in *Keiskea* and many species of *Elsholtzia* (e.g. *E. ciliata*, *E. luteola* (Fig. 27) and *E. stauntonii*). In the paniculate species of *Pogostemon* the verticils are sub-secund, i.e. the flowers are secundly arranged in each verticil but the verticils themselves are not secund on the stem. The flowers in all genera may be pedicellate or sessile.

Pollen

There is no complete pollen survey of the Pogostemoneae. However, sufficient data is available to make some considerations. Labiatae pollen is remarkably uniform and only two features, the number of colpi and the number of nuclei, show taxonomically useful variation. The pollen grains are either bi-nucleate and tri-colpate or tri-nucleate and hexa-colpate (see Erdtman, 1945, 1952). A number of authors (e.g. Wunderlich, 1963; El-Gazzar & Watson, 1968) have advanced the view that these characters have a high taxonomic value and have used them to good effect in studies on relationships within the Labiatae and closely related groups. Pollen from eight Pogostemoneae genera has been examined by other workers. To provide a full sample I examined *Eurysolen gracilis* and *Leucosceptrum canum* pollen under the light microscope. The data are summarized in Table 4.

Table 4 Numbers of nuclei and colpi in pollen grains of the Pogostemoneae.

Genus	Number of nuclei per cell	Number of colpi per cell
Elsholtzia	3	6
Keiskea	3	6
Tetradenia	3	6
Eurysolen	–	3
Comanthosphace	2	3
Leucosceptrum	–	3
Rostrinucula	2	3
Pogostemon	2	3
Dysophylla	2	3
Colebrookea	2	3

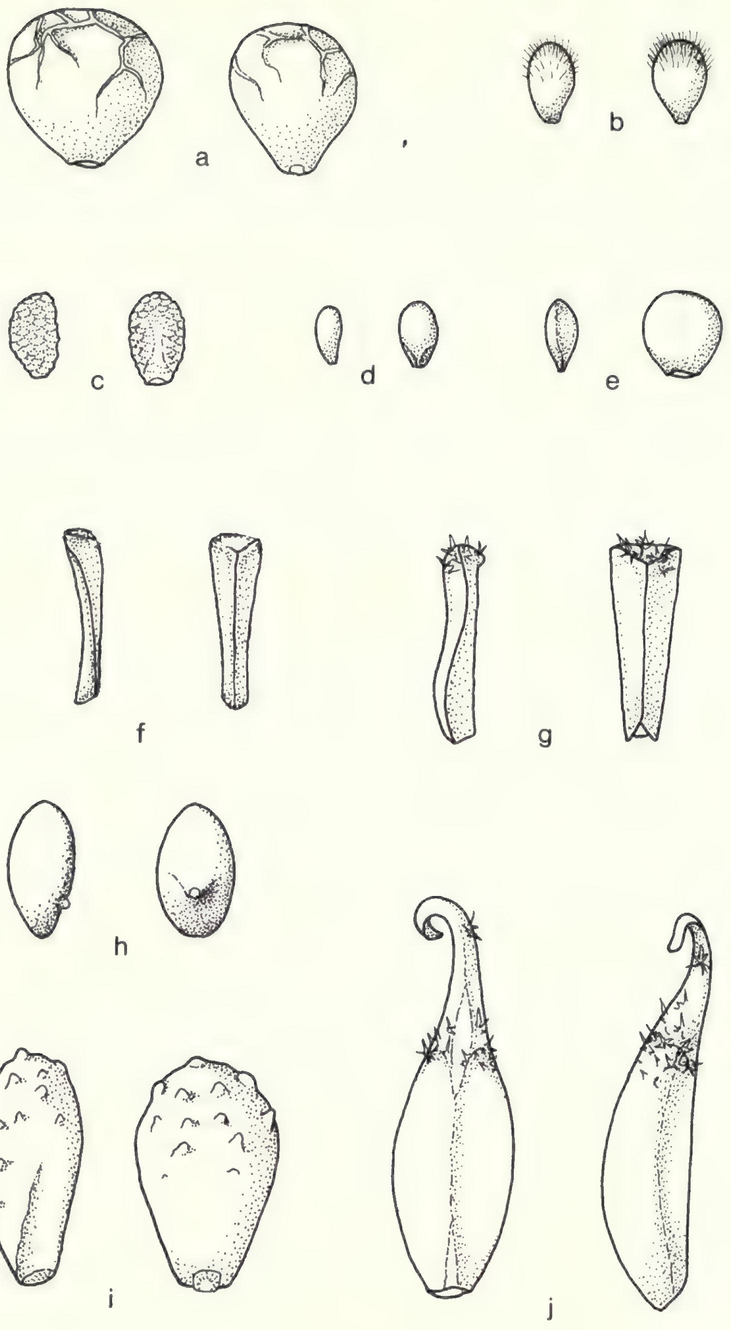


Fig. 10 Nutlet types in the Pogostemoneae. Profile and inner face of nutlet are shown. All × 10. (a) *Keiskea japonica.* (b) *Colebrookea oppositifolia.* (c) *Eurysolen gracilis.* (d) *Dysophylla stellata.* (e) *Pogostemon mollis.* (f) *Leucosceptrum canum.* (g) *Comanthosphace barbinervis.* (h) *Elsholtzia flava.* (i) *Elsholtzia densa.* (j) *Rostrinucula dependens.*

5. The analyses

Principal co-ordinates analysis

A general view of overall similarities can be obtained by looking at two-dimensional plots using the first four eigenvectors of the principal co-ordinates analysis (Figs 11–13). These vectors account for 43% of the total variation and although low, this percentage is sufficiently high to provide a basis for comparing the different groups.

The results show a clear division of the points into two major groups; one formed by *Dysophylla* and *Pogostemon*, the other containing the remaining taxa except *Colebrookea* and *Rostrinucula* which occupy intermediate positions between the two groups. *Comanthosphace* and *Leucosceptrum canum* (OTU 127) are rather peripheral members of the second group in Fig. 13, where they are quite distant from the main cluster.

Two OTUs are outstanding in their positions. *Dysophylla mairei* Léveillé (OTU 65) is clustered with *Elsholtzia*, while *Elsholtzia aquatica* (OTU 22) is clustered with *Dysophylla* and *Pogostemon*.

This separation into two major groups provides a convenient division for further investigation. Each group was used as a subset for which a second series of plots was prepared. *Colebrookea* and *Rostrinucula* were omitted from these plots.

Figs 14–16 show the plots for the *Comanthosphace/Elsholtzia* subset. *Comanthosphace* and *Leucosceptrum canum* (OTU 127) are separated from the main cluster of *Elsholtzia* species (Fig. 14). *Keiskea* and *Tetradenia* are also separated from *Elsholtzia* but only when the third (Fig. 15) and fourth (Fig. 16) eigenvectors are used.

Elsholtzia is divisible into two sub-groups, and this is more easily seen when only the species of *Elsholtzia* are marked on the plots (Figs 17–19). The first sub-group represents sections *Cyclostegia* and *Elsholtzia* and occupies that end of the cluster furthest away from *Comanthosphace*. The species forming these two sections are quite intermixed. The second sub-group represents section *Aphanochilus* series *Stenelasmeae* and occupies that part of the main cluster nearest to *Comanthosphace*. The two sub-groups are separated in the original plots (Figs 14–16) by *Keiskea* and *Tetradenia*.

Figs 17–19 show an interesting distribution for the three species of *Elsholtzia* section *Aphanochilus* series *Platyelasmeae*. *E. eriostachya* (OTU 19) consistently segregates with section *Aphanochilus* series *Stenelasmeae*, whilst *E. densa* (OTU 20) segregates with sections *Cyclostegia* and *Elsholtzia*. The third species, *E. manshurica* (Kitagawa) Kitagawa (OTU 21), occupies an intermediate position between the sub-groups, although in Fig. 17 it is part of the sections *Cyclostegia* and *Elsholtzia* sub-group. Note also the position of OTU 8, *E. concinna,* in each of the plots. In all analyses *Dysophylla mairei* (OTU 65), *Eurysolen gracilis* (OTU 1) and *Leucosceptrum plectranthoideum* (Léveillé) Marquand (OTU 128), remain within the sub-group formed by *Elsholtzia* section *Aphanochilus* series *Stenelasmeae*.

The analysis of the *Dysophylla/Pogostemon* subset is shown in Figs 20–22. These two genera form a single cluster within which is a marked distribution of points. Most *Dysophylla* species occupy one half of the cluster and *Pogostemon* occupies the other half. *Elsholtzia aquatica* (OTU 22) always clusters with *Dysophylla*.

Clustering to maximize within-group-mean-similarity (WGMS)

As an independant check to help decide which real groups may be present in the Pogostemoneae the data were analysed using a method for clustering to maximize WGMS. For this method the number of groups must be preselected (see p. 12) and here the similarity matrix was used as a guide. A pictorial representation of the similarity matrix was prepared by replacing the percentage similarities with appropriate symbols to make groups of similar OTUs more easily visible (Figs 23 and 24). There are two distinct patterns, one with six groups and a second with nine groups.

Allocating the OTUs among six groups yields little information. The WGMS and BGMS values (Table 5) are so close that, with the possible exception of group four—*Comanthosphace, Rostrinucula,* and *Leucosceptrum canum* (OTU 127), no discrete groups can be recognized.

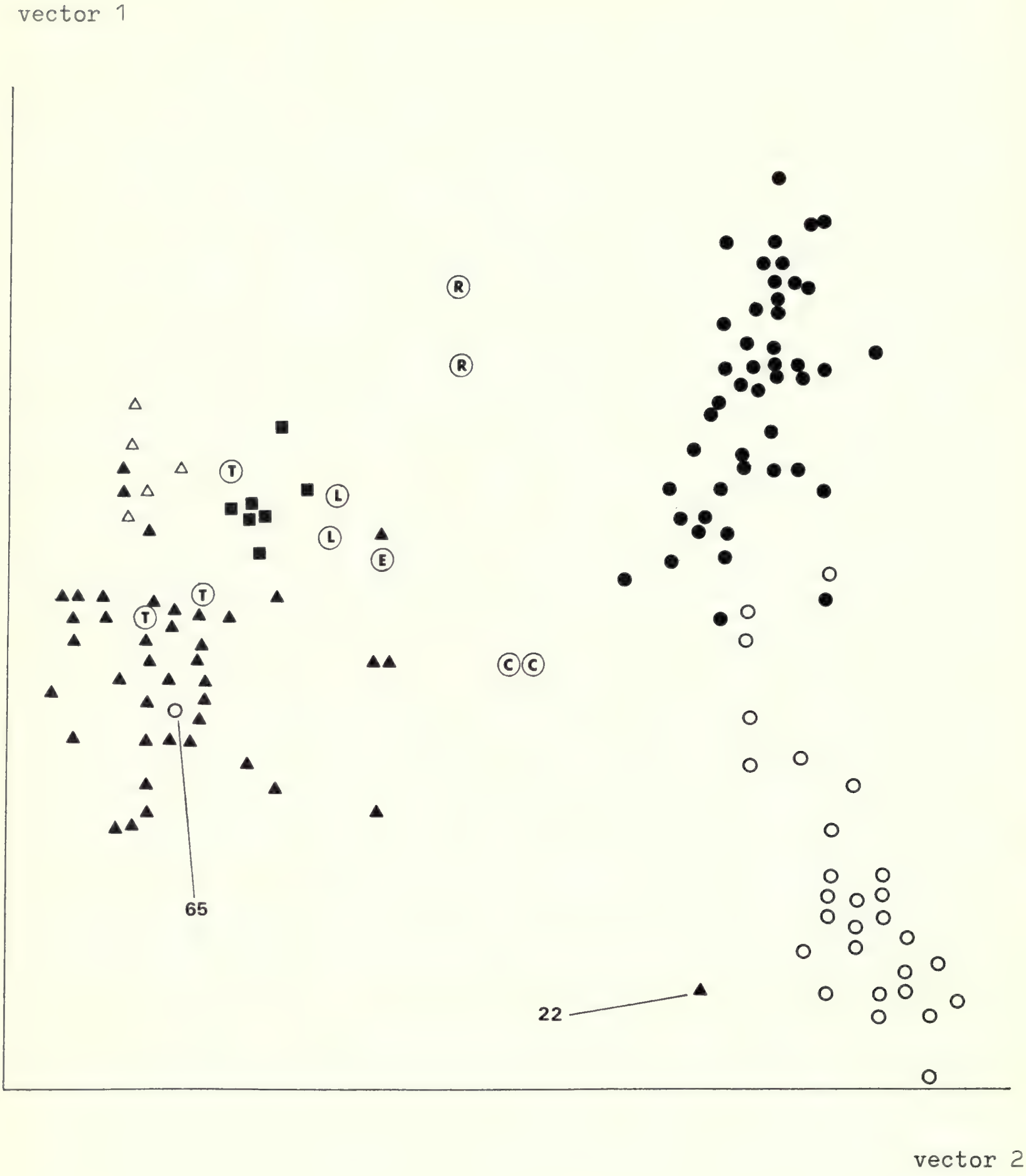


Fig. 11 Two-dimensional plot of the Pogostemoneae using principal co-ordinates analysis.
Key: *Pogostemon*, ●; *Dysophylla*, ○; *Elsholtzia*, ▲; *Comanthosphace*, ■; *Keiskea*, △; *Tetradenia*, Ⓣ; *Leucosceptrum*, Ⓛ; *Rostrinucula*, *Rostrinucula*, Ⓡ; *Colebrookea*, Ⓒ; *Eurysolen*, Ⓔ.

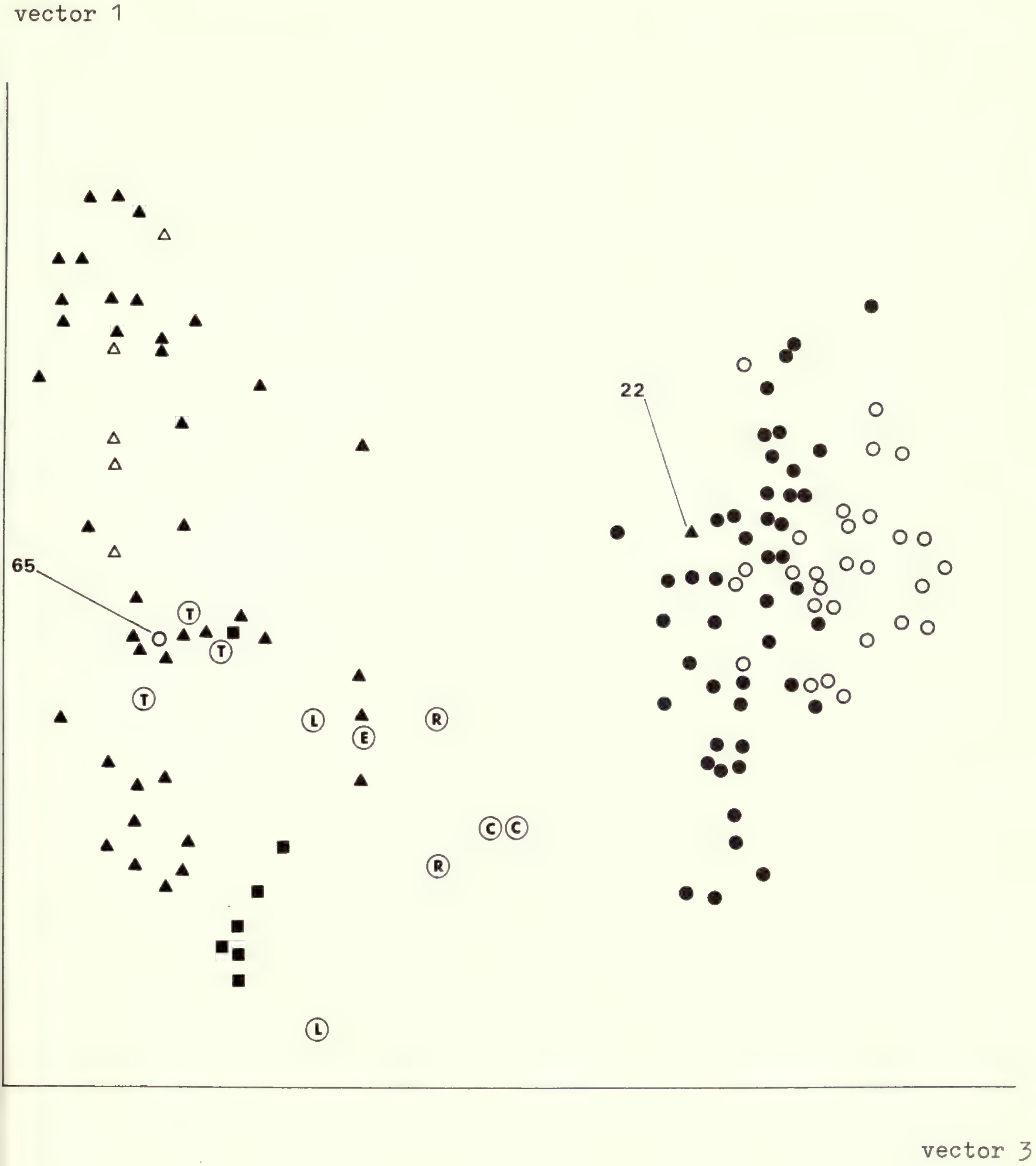


Fig. 12 Two-dimensional plot of the Pogostemoneae using principal co-ordinates analysis.
Key: *Pogostemon*, ●; *Dysophylla*, ○; *Elsholtzia*, ▲; *Comanthosphace*, ■; *Keiskea*, △; *Tetradenia*, Ⓣ; *Leucosceptrum*, Ⓛ; *Rostrinucula*, Ⓡ; *Colebrookea*, Ⓒ; *Eurysolen*, Ⓔ.

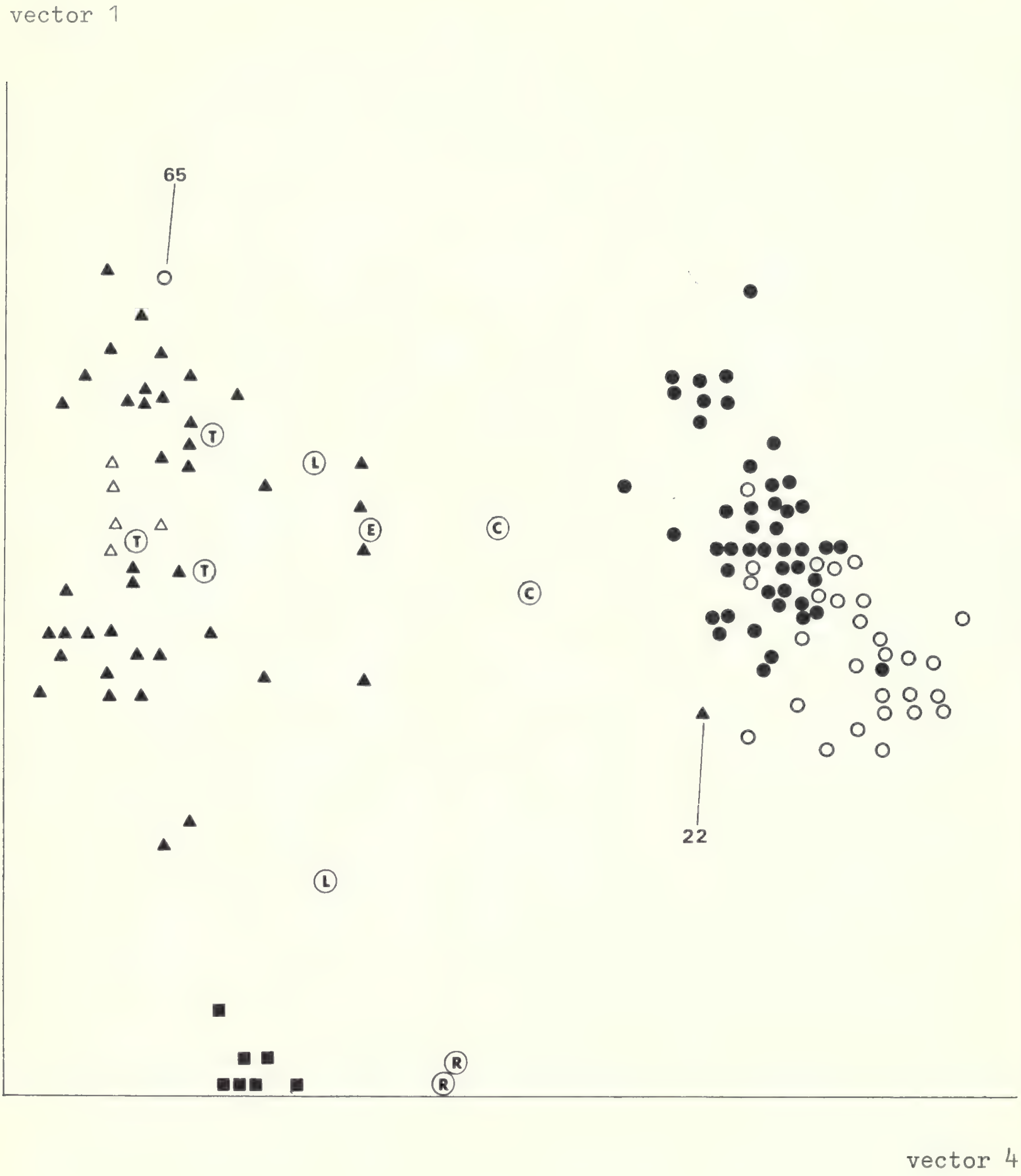


Fig. 13 Two-dimensional plot of the Pogostemoneae using principal co-ordinates analysis.
Key: *Pogostemon*, ●; *Dysophylla*, ○; *Elsholtzia*, ▲; *Comanthosphace*, ■; *Keiskea*, △; *Tetradenia*, Ⓣ; *Leucosceptrum*, Ⓛ; *Rostrinucula*, Ⓡ; *Colebrookea*, Ⓒ; *Eurysolen*, Ⓔ.

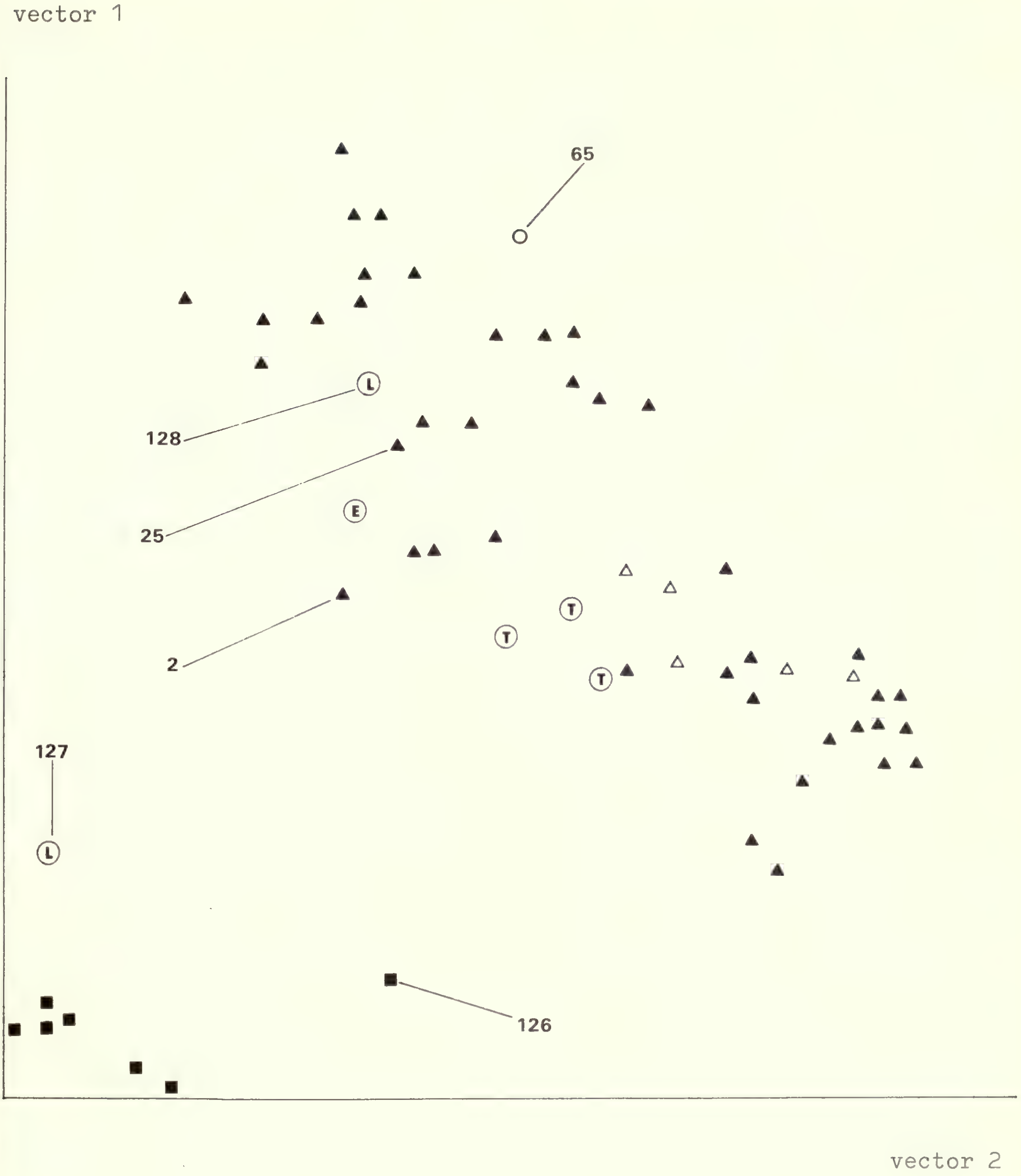


Fig. 14 Two-dimensional plot of the *Comanthosphace/Elsholtzia* subset using principal co-ordinates analysis.

Key: *Dysophylla*, ○; *Elsholtzia*, ▲; *Comanthosphace*, ■; *Keiskea*, △; *Tetradenia*, Ⓣ; *Leucosceptrum*, Ⓛ; *Eurysolen*, Ⓔ.

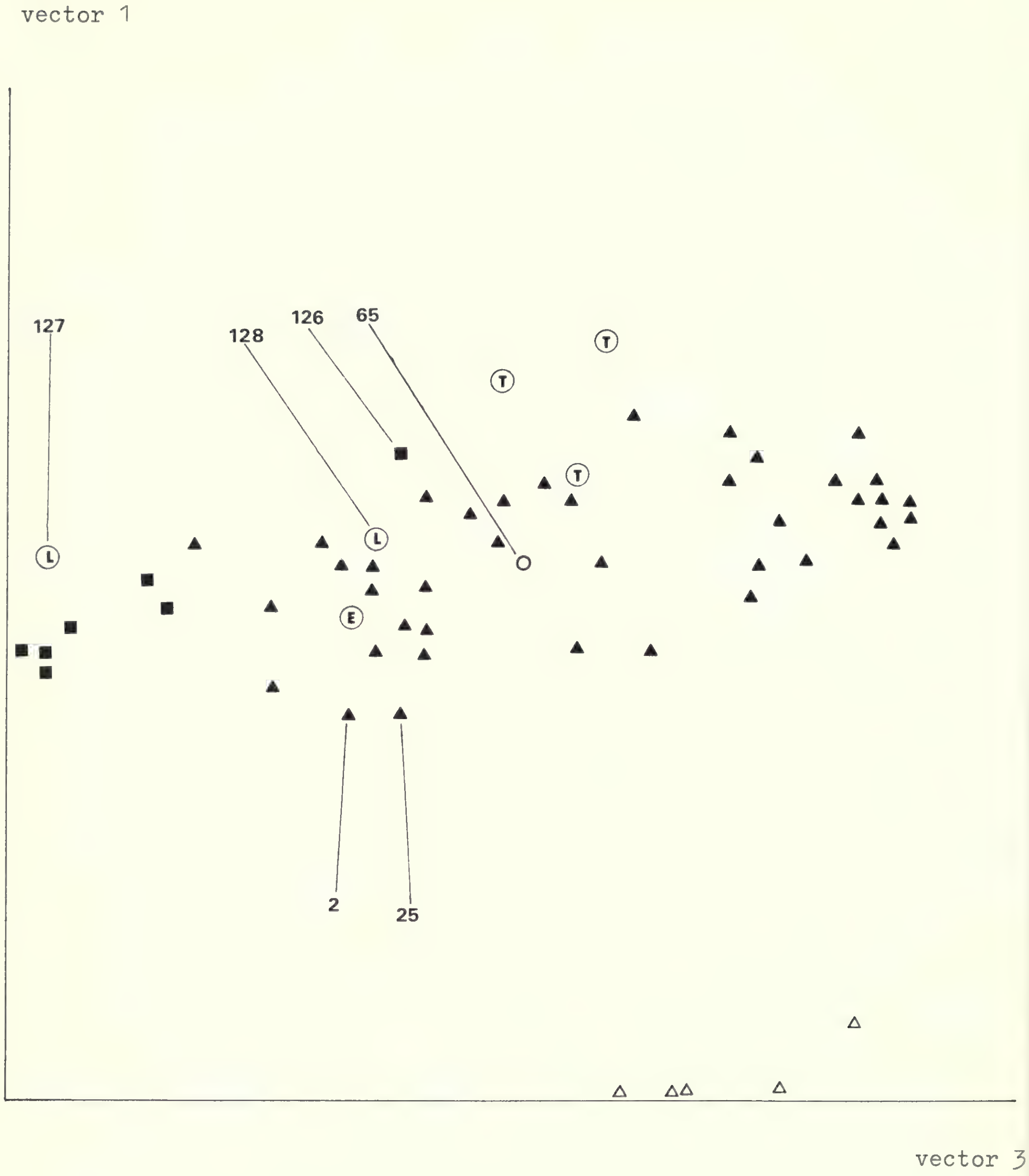


Fig. 15 Two-dimensional plot of the *Comanthosphace*/*Elsholtzia* subset using principal co-ordinates analysis.
Key: *Dysophylla*, ○; *Elsholtzia*, ▲; *Comanthosphace*, ■; *Keiskea*, △; *Tetradenia*, Ⓣ; *Leucosceptrum*, Ⓛ; *Eurysolen*, Ⓔ.

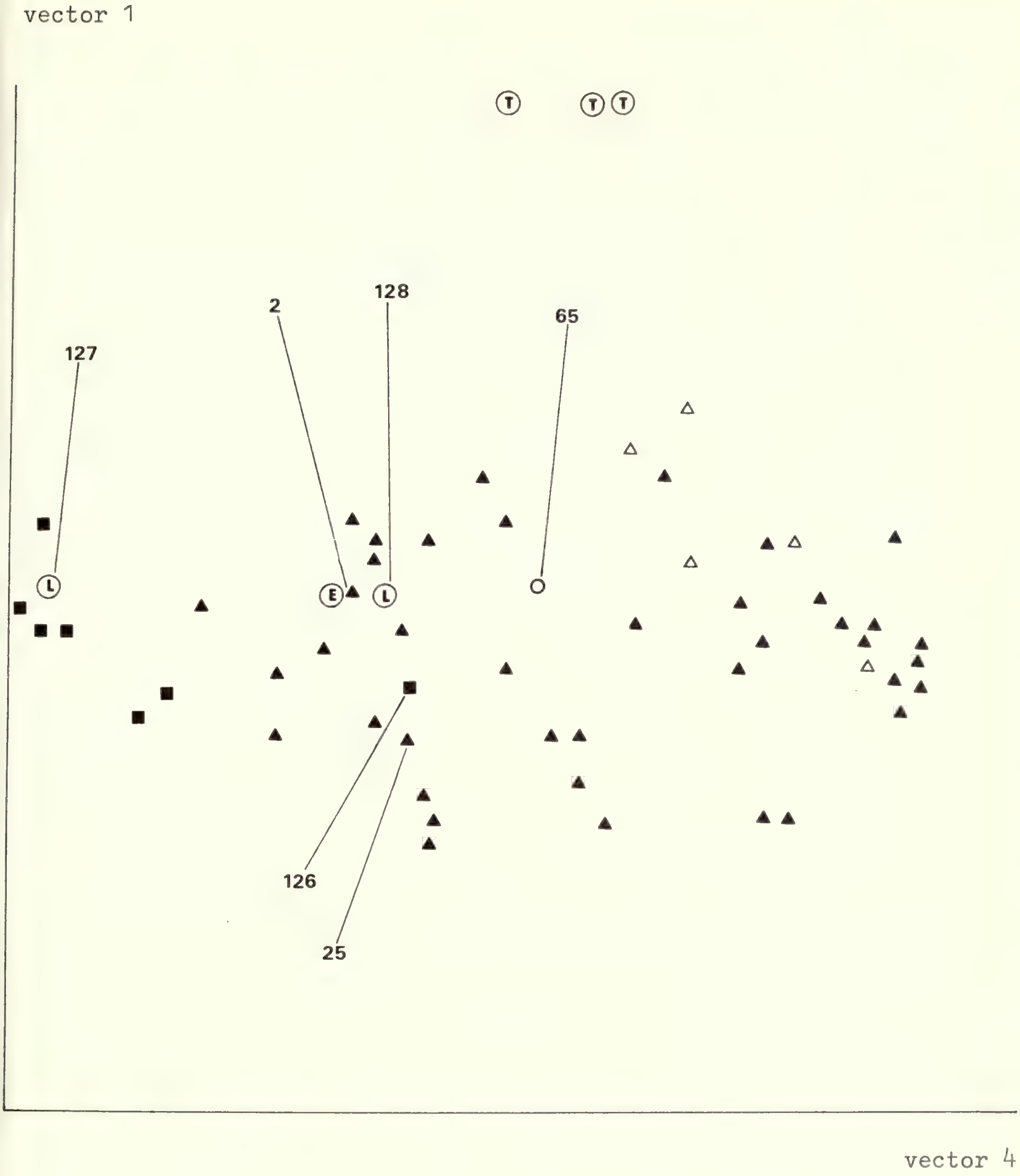


Fig. 16 Two-dimensional plot of the *Comanthosphace/Elsholtzia* subset using principal co-ordinates analysis.

Key: *Dysophylla*, ○; *Elsholtzia*, ▲; *Comanthosphace*, ■; *Keiskea*, △; *Tetradenia*, Ⓣ; *Leucosceptrum*, Ⓛ; *Eurysolen*, Ⓔ.

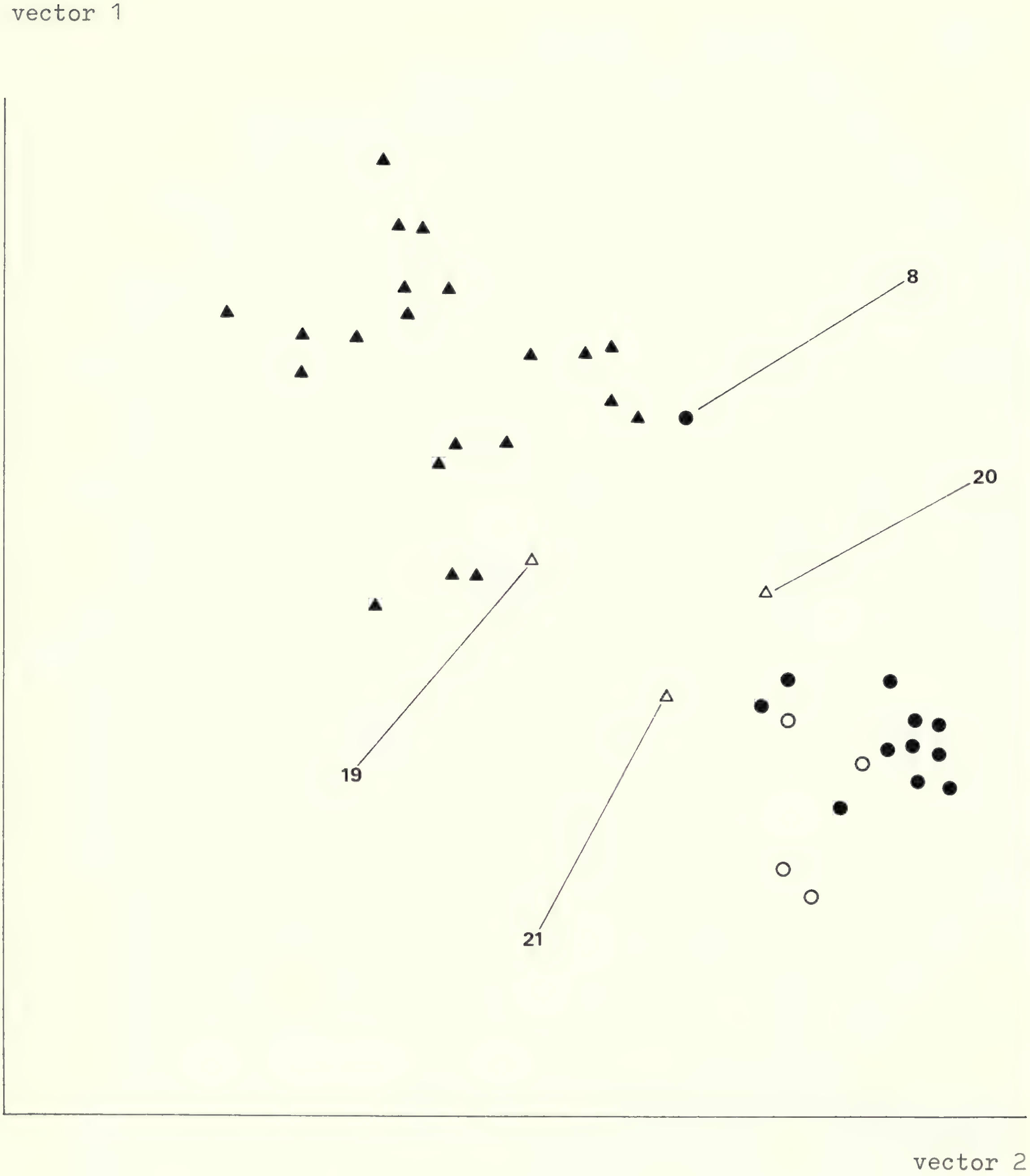


Fig. 17 Two-dimensional plot of the *Comanthosphace/Elsholtzia* subset showing the distribution of species of *Elsholtzia* only.
Key: Section *Elsholtzia* ●; Section *Cyclostegia* ○; Section *Aphanochilus* series *Stenelasmeae* ▲; Section *Aphanochilus* series *Platyelasmeae* △.

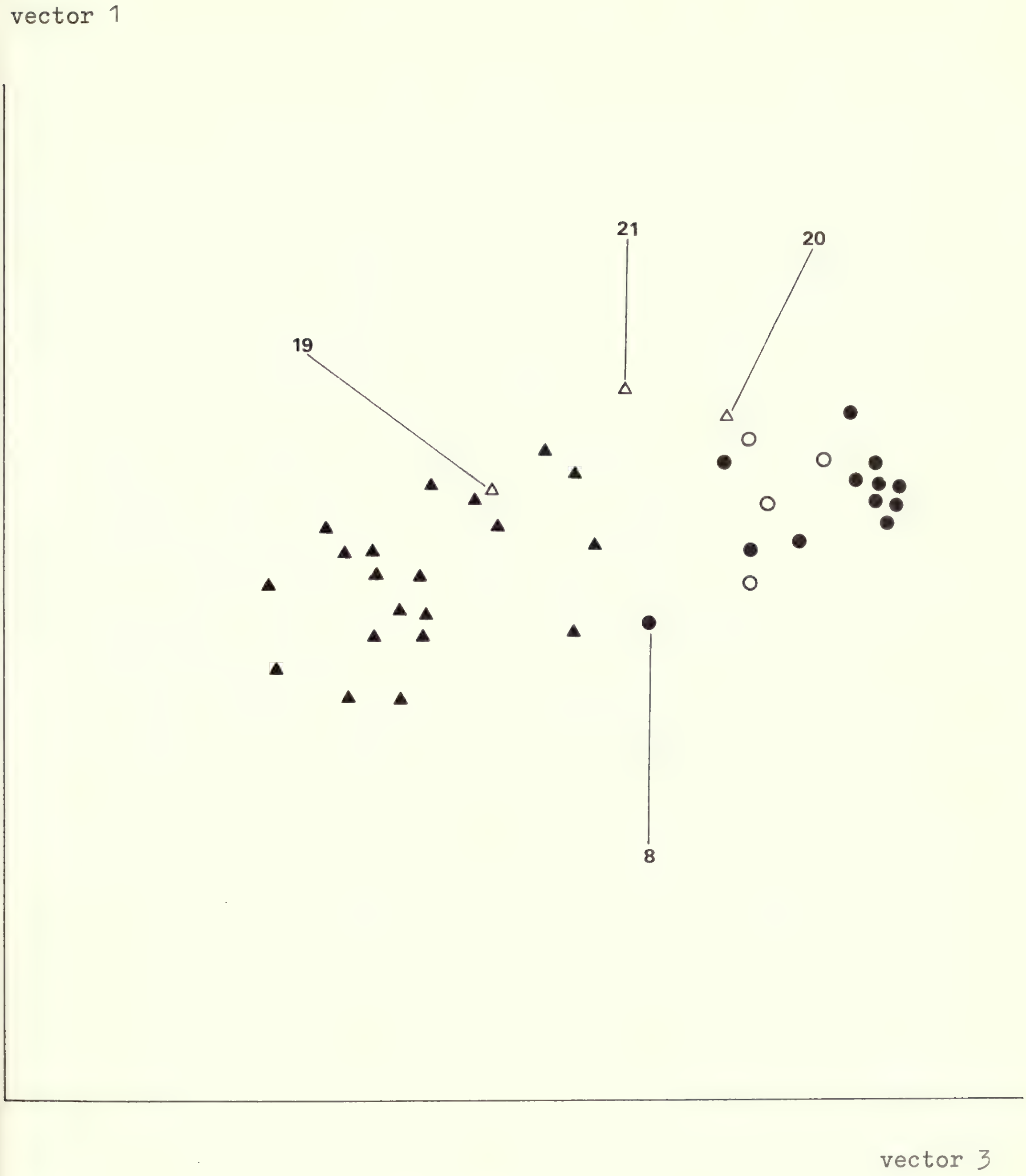


Fig. 18 Two-dimensional plot of the *Comanthosphace*/*Elsholtzia* subset showing the distribution of species of *Elsholtzia* only.
Key: Section *Elsholtzia* ●; Section *Cyclostegia* ○; Section *Aphanochilus* series *Stenelasmeae* ▲; Section *Aphanochilus* series *Platyelasmeae* △.

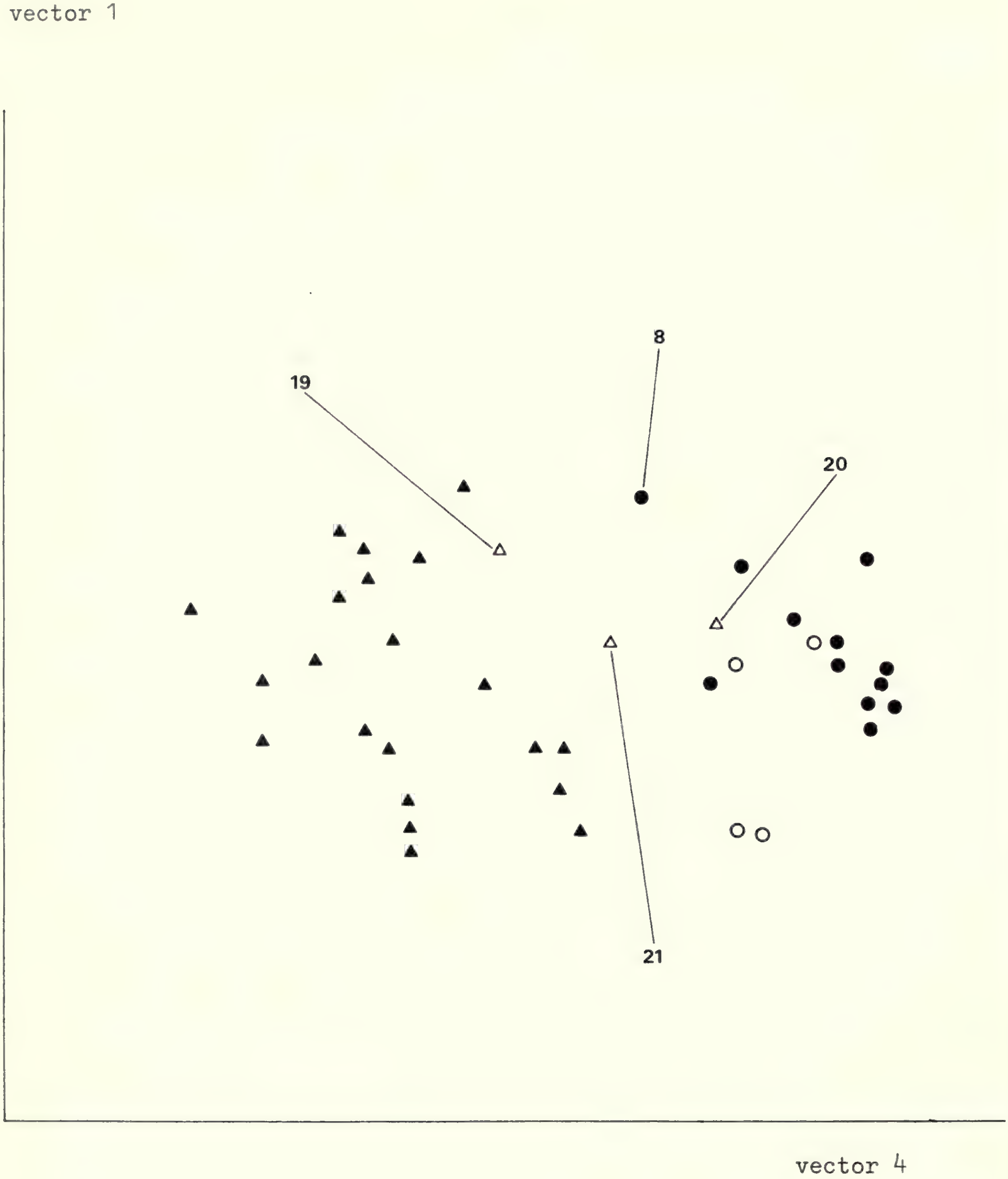


Fig. 19 Two-dimensional plot of the *Comanthosphace*/*Elsholtzia* showing the distribution of species of *Elsholtzia* only.
Key: Section *Elsholtzia* ●; Section *Cyclostegia* ○; Section *Aphanochilus* series *Stenelasmeae* ▲; Section *Aphanochilus* series *Platyelasmeae* △.

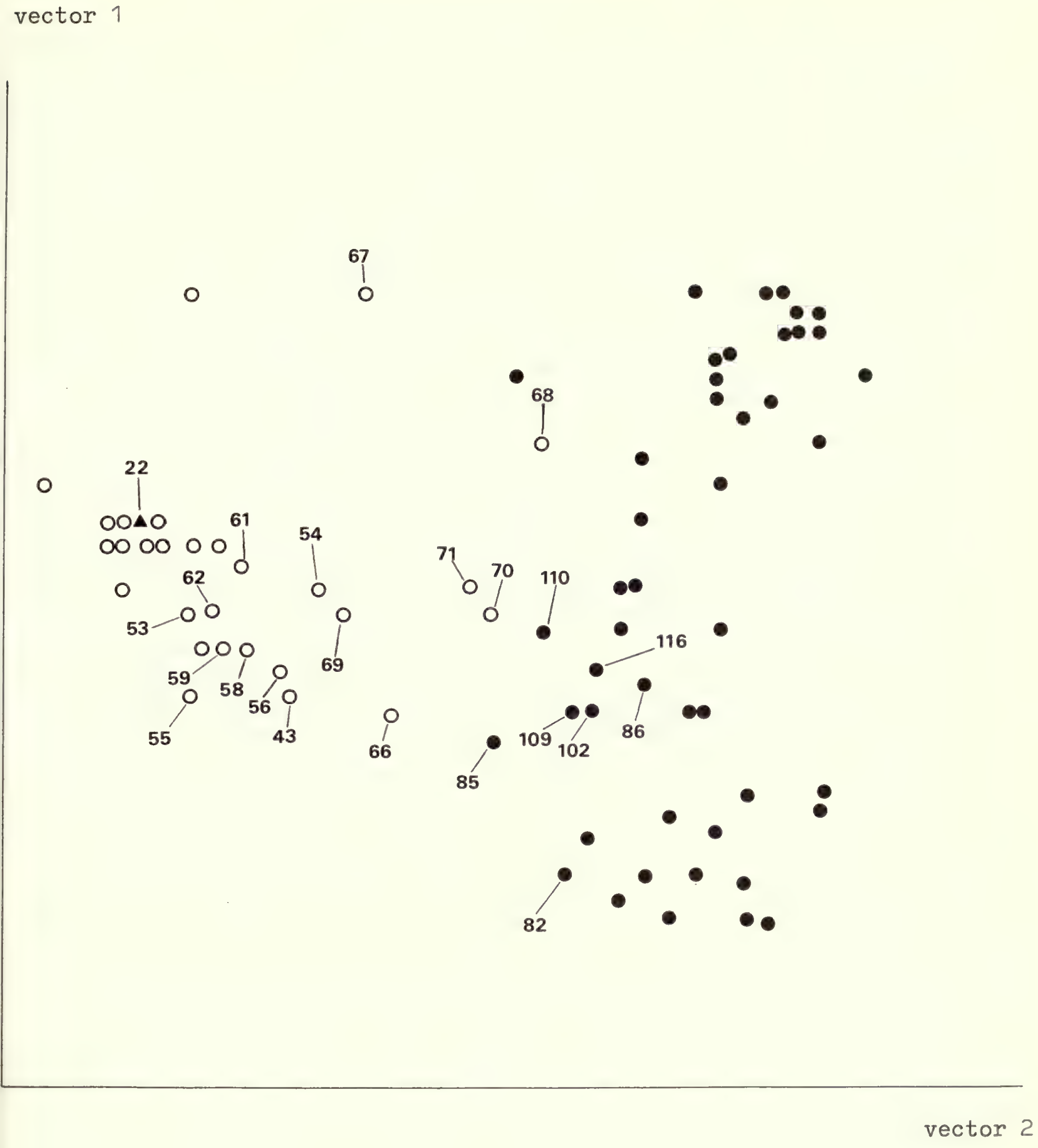


Fig. 20 Two-dimensional plot of the *Dysophylla*/*Pogostemon* subset using principal co-ordinates analysis.
Key: *Pogostemon*, ●; *Dysophylla*, ○; *Elsholtzia*, ▲.

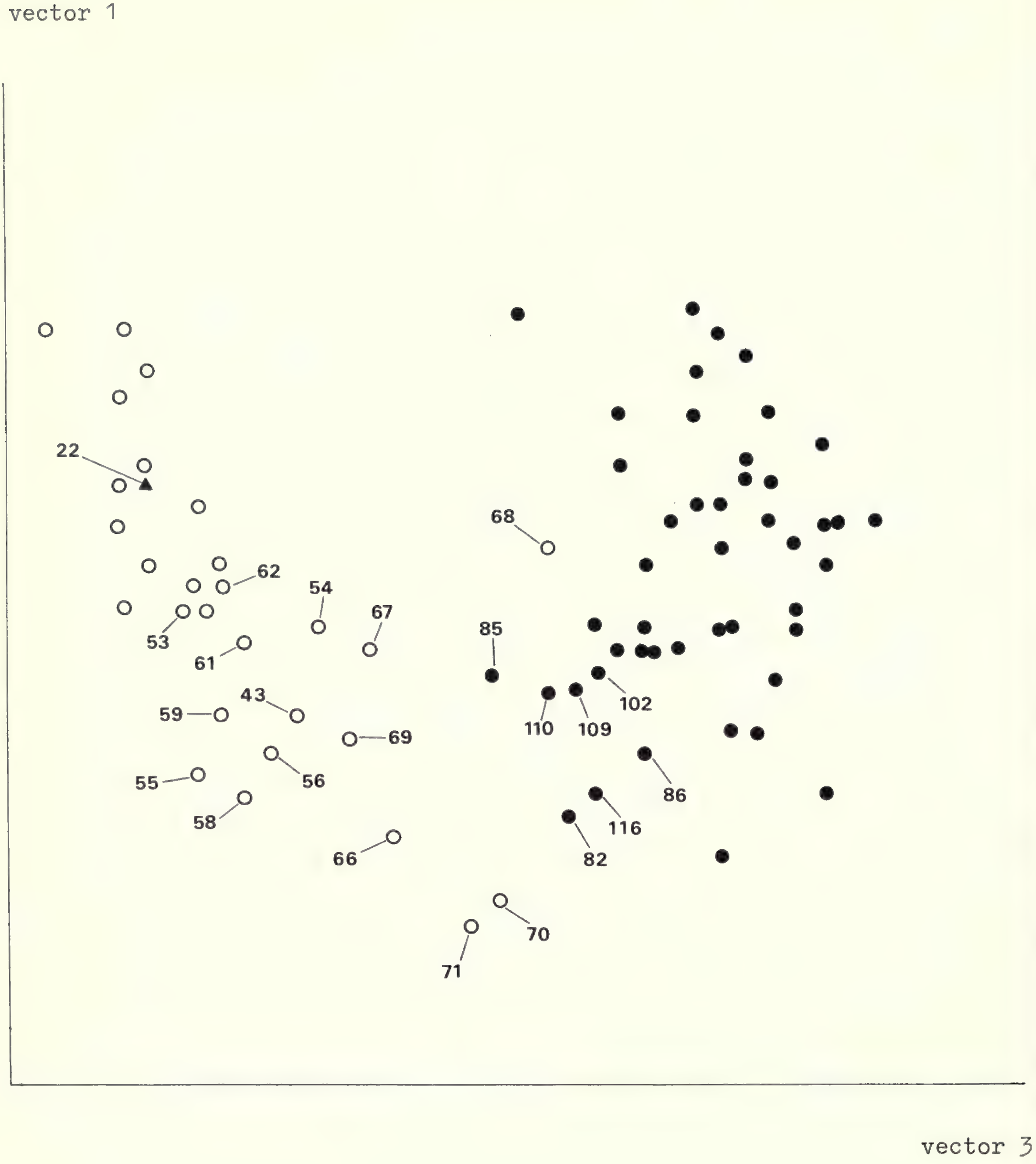


Fig. 21 Two-dimensional plot of the *Dysophylla*/*Pogostemon* subset using principal co-ordinates analysis. Key: *Pogostemon*, ●; *Dysophylla*, ○; *Elsholtzia*; ▲.

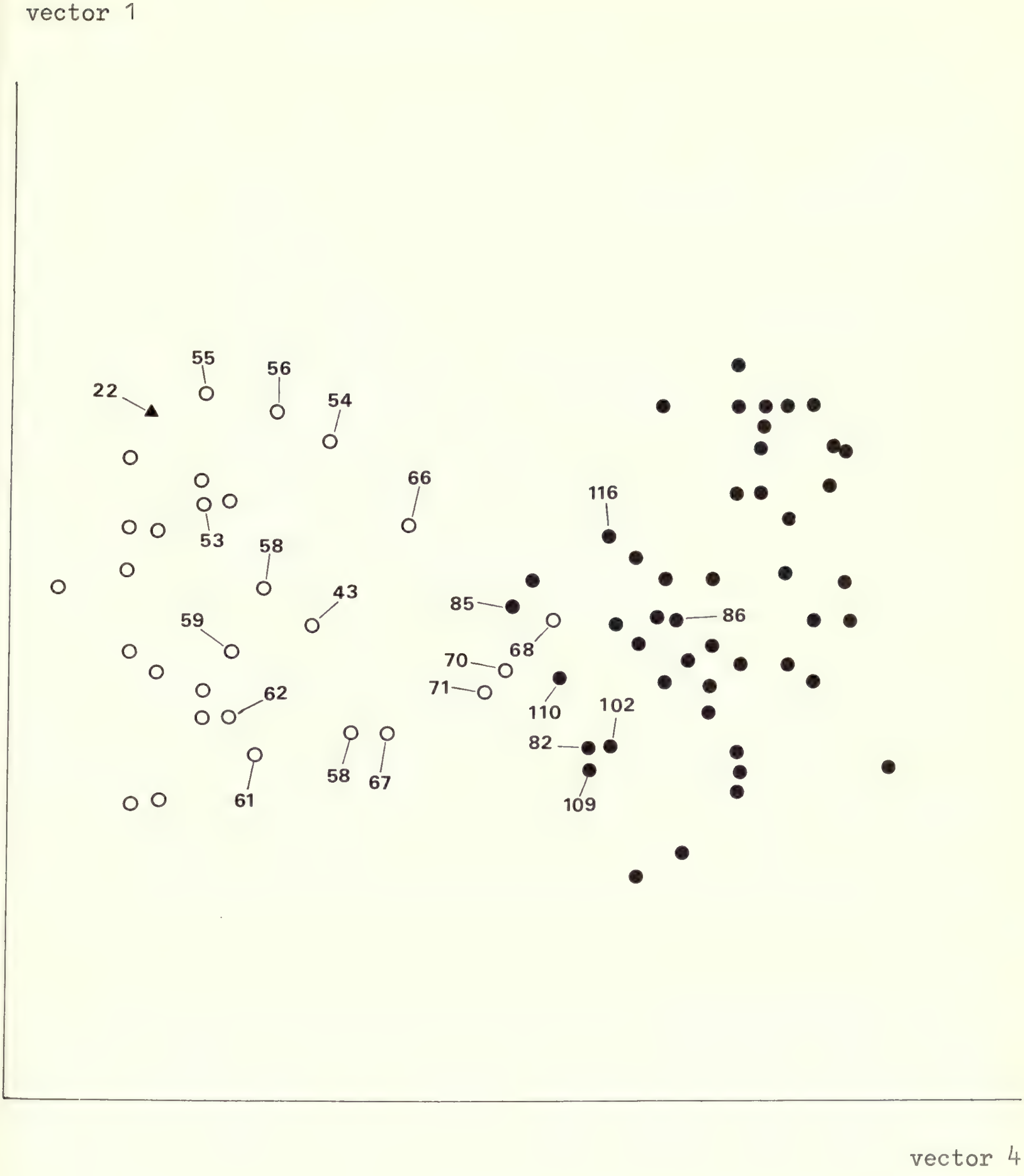


Fig. 22 Two-dimensional plot of the *Dysophylla/Pogostemon* subset using principal co-ordinates analysis.
Key: *Pogostemon*, ●; *Dysophylla*, ○; *Elsholtzia*, ▲.

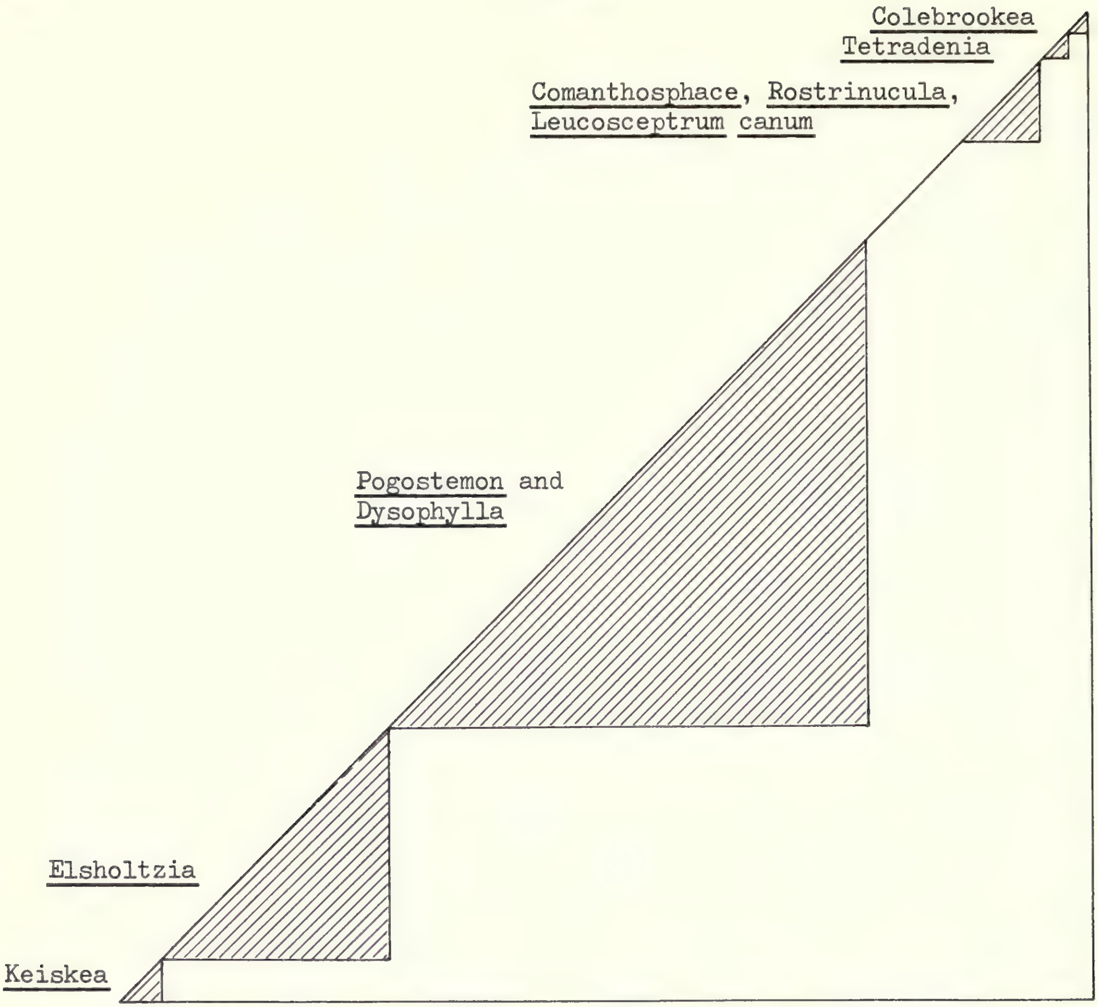


Fig. 23 Diagram showing six possible groups indicated in the similarity matrix.

Allocating the OTUs among nine groups (Table 6) is more informative and confirms the general picture obtained from the principal co-ordinates analyses. *Comanthosphace* and *Leucosceptrum canum* (OTU 127) are confirmed as forming a group separate from other OTUs but here the group includes *Rostrinucula*. As in the principal co-ordinates analysis (Figs 11–13) the remaining taxa (except *Colebrookea*) are divided into two subsets. The first contains groups four, five, and seven which share low BGMS values with the remaining groups, but high BGMS values with each other. *Dysophylla* section *Verticillatae* is placed in group four, but species of section *Oppositifoliae* are divided between all three groups, *D. salicifolia* (OTU 69) in group four, *D. myosuroides* (OTU 71) and *D. rugosa* (OTU 70) in group five, and *D. auricularia* (OTU 68) in group seven. *Elsholtzia aquatica* (OTU 22) is placed with *Dysophylla* section *Verticillatae* in group four. *Pogostemon* is divided between groups five and seven.

The second subset contains groups two, three, six, and nine, but groups two (*Keiskea*) and three (*Tetradenia*) are quite discrete. Not so *Elsholtzia* in groups six and nine, which share high

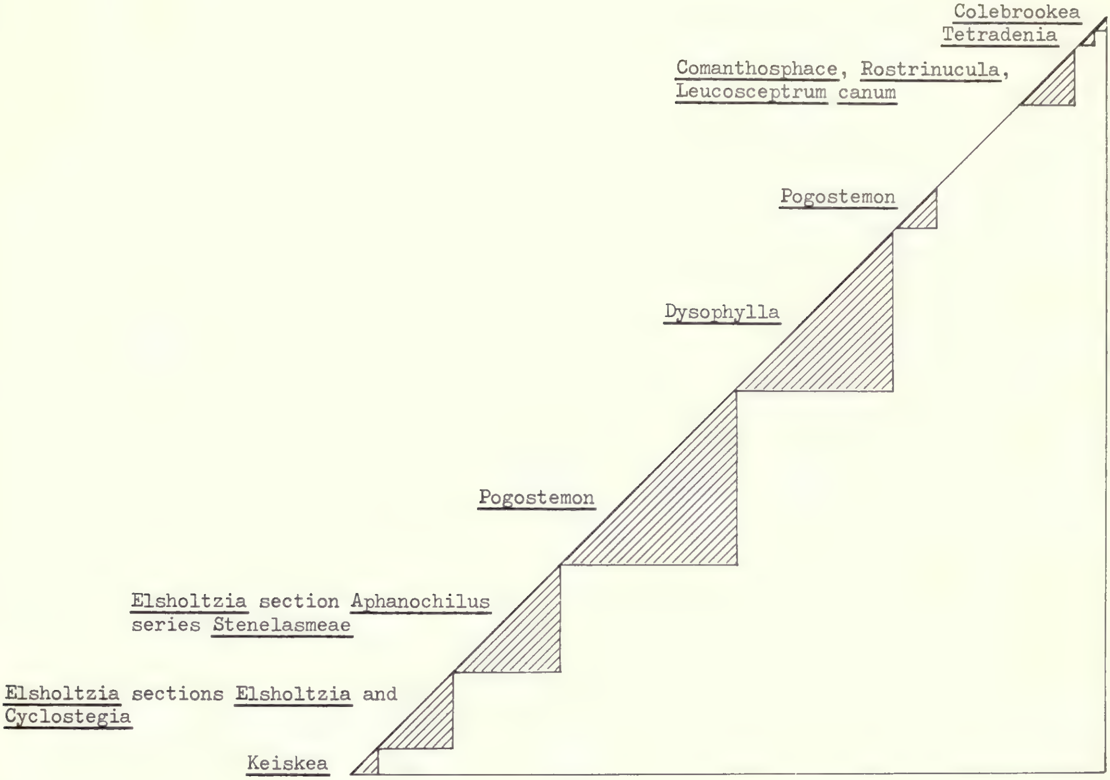

Colebrookea
Tetradenia
Comanthosphace, Rostrinucula,
Leucosceptrum canum
Pogostemon
Dysophylla
Pogostemon
Elsholtzia section Aphanochilus
series Stenelasmeae
Elsholtzia sections Elsholtzia and
Cyclostegia
Keiskea

Fig. 24 Diagram showing nine possible groups indicated in the similarity matrix.

BGMS values compared to their respective WGMS values. Group six contains *Elsholtzia* section *Aphanochilus* series *Stenelasmeae* together with *E. eriostachya* (OTU 19) from series *Platyelasmeae* and *E. concinna* (OTU 8). Once again *Dysophylla mairei* (OTU 65), *Eurysolen gracilis* (OTU 1), and *Leucosceptrum plectranthoideum* (OTU 128) are all included in this group. Group nine contains *Elsholtzia* sections *Cyclostegia* and *Elsholtzia* plus *E. densa* (OTU 20) and *E. manshurica* (OTU 21) of *Elsholtzia* section *Aphanochilus* series *Platyelasmeae*.

Group eight is an anomaly, containing the unlikely combination of *Colebrookea* with one species each of *Dysophylla* and *Pogostemon*. The heterogeneity of this combination is reflected in the very low WGMS value of 79·3% and the obvious similarity with *Dysophylla* and *Pogostemon* in groups four, five, and seven. A slight rearrangement of the OTUs to remove the anomaly results in the similarities shown in Table 7. Here the species of *Dysophylla* and *Pogostemon* are removed, '*Dysophylla glabrata*' (OTU 67) now placed in group four and

Table 5 WGMS and BGMS values for six groups in the clustering to maximize WGMS analysis.

1	84·8					
2	82·4	88·9				
3	73·7	72·0	79·7			
4	71·6	70·4	72·1	85·8		
5	82·3	81·4	70·9	71·2	87·9	
6	80·8	78·8	70·1	67·7	76·4	88·3
	1	2	3	4	5	6

Key to groups:
1—*Colebrookea,* species of *Pogostemon,* and *Dysophylla* section *Oppositifoliae.*
2—species of *Pogostemon.*
3—*Keiskea, Tetradenia, Elsholtzia* and *Eurysolen.*
4—*Comanthosphace, Rostrinucula* and *Leucosceptrum canum.*
5—species of *Pogostemon.*
6—*Dysophylla* section *Verticillatae.*
(For exact distribution of OTUs see Appendix 4.)

Table 6 WGMS and BGMS values for nine groups in the clustering to maximize WGMS analysis.

1	85·8								
2	67·9	90·8							
3	70·3	70·2	94·7						
4	67·9	64·2	65·8	88·8					
5	71·8	69·3	70·4	80·0	85·8				
6	72·6	74·8	74·0	71·8	74·3	83·1			
7	70·7	70·0	68·0	78·9	83·0	72·2	89·6		
8	67·2	65·8	66·7	75·4	73·8	71·3	76·5	79·3	
9	72·8	77·3	76·4	70·8	72·2	78·3	73·0	68·5	86·7
	1	2	3	4	5	6	7	8	9

Key to groups:
1—*Comanthosphace, Rostrinucula,* and *Leucosceptrum canum.*
2—*Keiskea.*
3—*Tetradenia.*
4—*Dysophylla* section *Verticillatae.*
5—species of *Pogostemon* and *Dysophylla* section *Oppositifoliae.*
6—*Elsholtzia* section *Aphanochilus* and *Eurysolen.*
7—species of *Pogostemon.*
8—*Colebrookea, 'Dysophylla glabrata',* and *Pogostemon amarantoides.*
9—*Elsholtzia* sections *Cyclostegia* and *Elsholtzia.*
(For exact distribution of OTUs see Appendix 4.)

Pogostemon amarantoides (OTU 80) in group seven. These transfers produce only small changes in the similarity values for these groups but the effect on group eight is striking. The WGMS rises to 95·2% and the links with groups four, five, and seven are greatly reduced.

Single-linkage analysis

In broad terms the single-linkage analysis reproduces the groupings given by the PCA and WGMS analyses but some minor deviations are of interest. *Colebrookea, Keiskea,* and *Tetradenia* form discrete groups in the dendrogram (Fig. 25). *Elsholtzia* can be divided into two subgroups, sections *Cyclostegia/Elsholtzia* and section *Aphanochilus* series *Stenelasmeae.* However, section *Aphanochilus* series *Platyelasmeae* is noticeably separate from the remainder of *Elsholtzia,* and for the first time *Eurysolen gracilis* (OTU 1) is separated from *Elsholtzia* section *Aphanochilus* series *Stenalasmeae. Dysophylla* and *Pogostemon* are very similar to each other, linking at, or above, the 91% level; *Dysophylla* section *Verticillatae* forms a subgroup but

Table 7 Adjusted WGMS and BGMS values for nine groups in the clustering to maximize WGMS analysis.

	1	2	3	4	5	6	7	8	9
1	88·5								
2	69·5	90·8							
3	71·3	70·2	94·7						
4	68·1	64·2	65·8	88·8					
5	68·9	69·3	70·4	80·0	85·8				
6	74·0	74·8	74·0	71·8	74·3	83·1			
7	67·4	70·0	68·0	78·9	83·0	72·2	89·6		
8	68·5	65·4	70·3	65·4	71·6	72·2	69·4	95·2	
9	73·9	77·3	76·4	70·8	72·2	78·3	73·0	67·1	86·7

Key to groups:
1—*Comanthosphace* and *Leucosceptrum canum.*
2—*Keiskea.*
3—*Tetradenia.*
4—*Dysophylla* section *Verticillatae.*
5—species of *Pogostemon* and *Dysophylla* section *Oppositifoliae.*
6—*Elsholtzia* section *Aphanochilus* and *Eurysolen.*
7—species of *Pogostemon.*
8—*Colebrookea.*
9—*Elsholtzia* sections *Cyclostegia and* Elsholtzia.

species of section *Oppositifoliae* are scattered among the species of *Pogostemon. Comanthosphace, Leucosceptrum canum* (OTU 127) and *Rostrinucula* form a group but with *C. nanchuanensis* (OTU 126), *L. canum* and *Rostrinucula* linking at low similarities. *Dysophylla mairei* (OTU 65) and *Leucosceptrum plectranthoideum* (OTU 128) link with *Elsholtzia* at high similarity levels. *Elsholtzia aquatica* (OTU 22) links with *Dysophylla* and *Pogostemon* at a somewhat lower similarity.

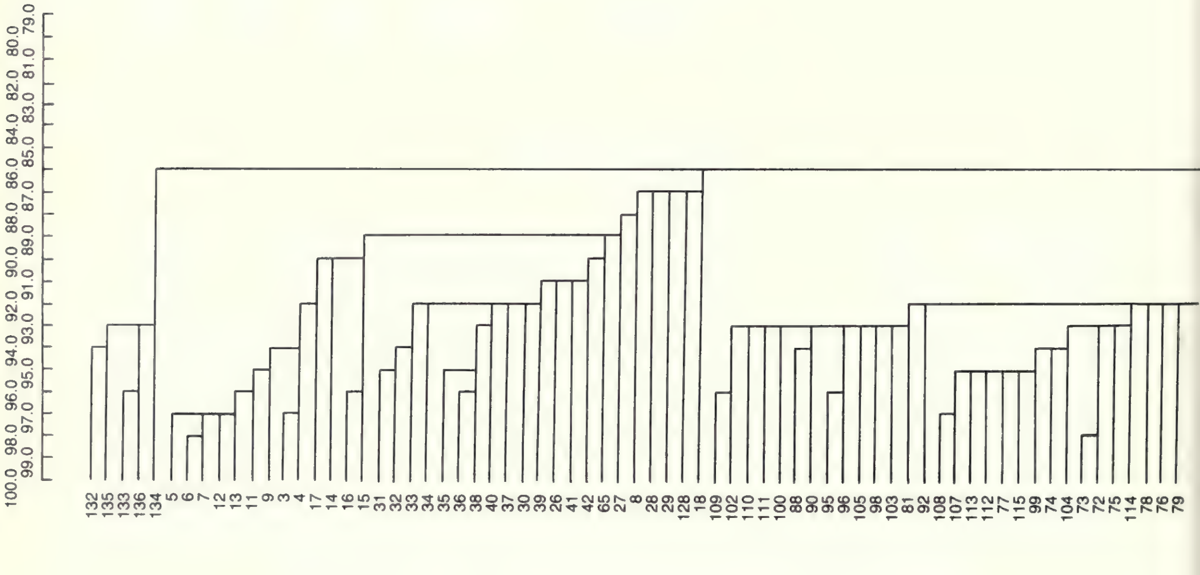
6. The taxa: discussion

Comanthosphace and *Leucosceptrum*

Comanthosphace, Rostrinucula, and *Leucosceptrum canum* form a rather complex group. *Rostrinucula* is discussed separately on p. 47 and *Leucosceptrum plectranthoideum* (OTU 128) is discussed on p. 57. Six species of *Comanthosphace* are morphologically very similar and are always closely grouped together. The seventh species, *C. nanchuanensis* (OTU 126), is much less similar to the other six and less obviously a member of the group, especially as shown by the second principal co-ordinates analysis (Figs 14–16) and the single-linkage dendrogram (Fig. 25). *Leucosceptrum canum* (OTU 127) is most similar to species of *Comanthosphace* but, like *C. nanchuanensis,* tends to lie on the fringe of the main group.

Comanthosphace can be recognized by a number of characters and character combinations. The most obvious and consistent are the broad, membranous, deciduous bracts and narrow, deciduous bracteoles, the closed annulus of hairs within the corolla, the hairy nutlets, and the dense pubescence of branched and unbranched hairs on all parts of the plant. Also, the flowers are large with relatively short, more or less equal calyx teeth, the upper lobe of the corolla is emarginate, and the anthers are unilocular.

Comanthosphace nanchuanensis appears to lack bracteoles although this is uncertain since both bracts and bracteoles fall very early and are not present on every specimen in related species. Similarly, the glabrous appearance of the nutlets may be recorded erroneously since no fully mature nutlets were available. The annulus within the corolla is incomplete. All the other characters distinguishing *Comanthosphace* are shared by *C. nanchuanensis* and the inclusion of this species within the *Comanthosphace* group seems intrinsically correct. Certainly the difference in overall similarity between *Comanthosphace pro majore* and *C. nanchuanensis* is not sufficiently great to justify the removal of the latter to a separate genus.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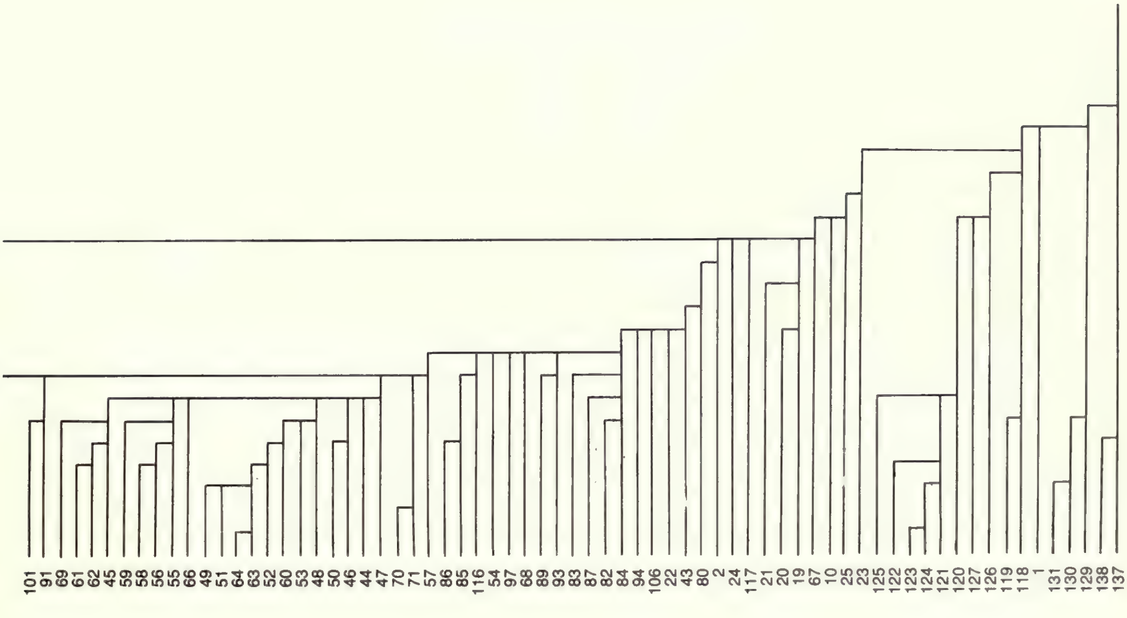
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118
1
131
130
129
138
137

Fig. 25 Single linkage dendrogram for 138 OTUs.

Leucosceptrum canum differs from *Comanthosphace* in two similar characters as *C. nanchuanensis.* Bracteoles are present, but there are no annular hairs within the corolla, and the nutlets are glabrous. Also, it has a terminal style whereas all species of *Comanthosphace,* including *C. nanchuanensis*, have gynobasic styles. With the exception of the style character *Leucosceptrum canum* is scarcely less similar to *Comanthosphace* than *C. nanchuanensis*, as shown by the similarities in Tables 8 and 9; thus *Comanthosphace* might easily be expanded to include it.

Table 8 WGMS and BGMS values for *Comanthosphace, Rostrinucula,* and *Leucosceptrum canum.*

1	93·7		
2	81·6	94·8	
3	84·3	72·3	100
	1	2	3

Key to groups:
1—*Comanthosphace.*
2—*Rostrinucula.*
3—*Leucosceptrum canum.*

Table 9 WGMS and BGMS values for *Comanthosphace, Rostrinucula,* and *Comanthosphace nanchuanensis.*

1	93.7		
2	81·6	94·8	
3	81·6	82·6	100
	1	2	3

Key to groups:
1—*Comanthosphace.*
2—*Rostrinucula.*
3—*Comanthosphace nanchuanensis.*

The gynobasic versus terminal style character is considered by most authors to be one of a number of heavily weighted characters distinguishing taxa at the tribal level. The analyses used here are all unweighted methods giving less consideration to characters of supposed high taxonomic value, such as those of the style, and thus raising the similarity between *Leucosceptrum canum* and *Comanthosphace.* Many authors unquestionably accept the value of the gynobasic versus terminal style characters, especially in studies of the Labiatae and Verbenaceae. I remain unsure of the absolute discrimination of these character states because the style type and nutlet attachment are not easily or clearly interpreted, at least for some species of the Pogostemoneae.

The style character is linked with a nutlet character so that in the gynobasic condition the nutlets have a small basal attachment scar; in the terminal condition the nutlets have a large lateral attachment scar. A terminal style and lateral attachment scar are a characteristic of the Labiatae tribe Ajugeae, and on this basis *Leucosceptrum canum* is usually placed in that group. In most species this pairing of style and nutlet characters holds true, but in others the link appears to break down. For example in *Elsholtzia densa* (OTU 20), (Figs 9, 10, 28) the style is gynobasic but the nutlets have a relatively large, somewhat oblique scar; in *E. flava* (OTU 28) the style is apparently gynobasic and the nutlet scars small but clearly lateral (Figs 9, 10). In *Leucosceptrum canum* (Fig. 9) the style is not always obviously terminal, sometimes appearing to rise almost directly from the disc. This divergence from the defined condition is reinforced by the nutlet scars which are small and basal. In this respect they are very similar to the nutlets of species of *Comanthosphace* (Fig. 10).

The nutlet characters may have been wrongly assessed in *Leucosceptrum canum*, a claim which has already been made by Kitamura & Murata (1962). However, they failed to take into account the apparent disparity of style characters between the tribe Ajugeae and the tribe to which they transferred *Leucosceptrum*, the Satureieae.

A more detailed study of gynobasic versus terminal styles in a wide range of species is required to assess the variation and importance of this character in the Labiatae. Should the style character prove to be less important than supposed, *Comanthosphace* and *Leucosceptrum* show sufficient overall morphological similarity to be considered congeneric. However, until the style character is reassessed, no conclusive statement can be made.

Rostrinucula

Rostrinucula dependens (OTU 118, Fig. 26) was originally described as *Elsholtzia dependens* by Rehder (1917) who stated that it seemed 'not closely related to any other species of the genus'. My studies also suggest weak links with *Elsholtzia*. Instead, the phenetic affinities of *Rostrinucula* lie with *Comanthosphace* and *Leucosceptrum canum*, these taxa being constantly linked with it. Indeed, *Rostrinucula sinensis* (OTU 119) was originally described by Hemsley as *Leusceptrum sinense*, only recently being recognized as a species of *Rostrinucula* by Wu (1965).

Confirmation of Kudo's (1929) separation of *Rostrinucula*, with bi-nucleate and tri-colpate pollen, from *Elsholtzia*, with tri-nucleate and hexa-colpate pollen, has already been pointed out by Wunderlich (1963). The pollen characters (Table 4) also confirm my placing of *Rostrinucula* with *Comanthosphace* and *Leucosceptrum*, which also have bi-nucleate and tri-colpate pollen.

Rostrinucula bears a striking overall resemblance to *Comanthosphace,* particularly in the long flower spikes with their broad, membranous, deciduous bracts and in the whitish indumentum of unbranched and branched hairs which cover all parts of the plant. The calyces are of similar size and shape, as are the corollas, and species of both genera have unilocular anthers, hairy nutlets, and lack a tumescent gland on the disc. Since these are all characters which distinguish *Comanthosphace* and *Leucosceptrum* from other genera within the Pogostemoneae the phenetic affinities of *Rostrinucula* lie here.

Rostrinucula, however, does not share all the characters of the *Comanthosphace/Leucosceptrum* group. Some features found in *Rostrinucula* are unique within the Pogostemoneae while others, although occurring elsewhere in the tribe, are not found in *Comanthosphace* or *Leucosceptrum.*

Rostrinucula dependens was named for its nutlets, each possessing a long curved beak at maturity (Figs 10, 26). Wu (1965) described the nutlets of *R. sinensis* as rostrate. In both species of *Rostrinucula* (Figs 7, 26) the annulus of hairs within the corolla is incomplete, unlike that of *Comanthosphace.* The hairs are borne on swollen disc-like excrescences at the base of the anther filaments and on the inner surface of a crescent-shaped invagination below the base of the lower lip. An identical arrangement is found in *Eurysolen gracilis* (OTU 1) (Figs 7, 29).

Rostrinucula differs from *Comanthosphace, Elsholtzia* and *Leucosceptrum* by the entire upper lip of the corolla (Fig. 7). In this respect only *Rostrinucula* more closely resembles *Dysophylla* and *Pogostemon.*

Rostrinucula is so closely linked with *Comanthosphace* in particular that the two might be considered congeneric. However, the species of *Rostrinucula* are less similar to *Comanthosphace* than is *Leucosceptrum canum* (OTU 127) (see Table 8 and Fig. 25), and they are readily distinguished by the nutlet and corolla characters given above.

Elsholtzia

The results of the analyses show that the species of *Elsholtzia* can be regarded as forming one group embracing all but one taxon, *E. aquatica* (OTU 22), or alternatively they can be regarded as two or three groups sharing high BGMS values. *E. aquatica*, which is now considered to be a species of *Pogostemon* (see pp. 64 & 66), is omitted from the following discussion. The clustering to maximize WGMS analysis (Tables 5–7) shows one or two groups. The principal co-ordinates analysis (Figs 14–19) shows one main group containing two sub-groups, whilst the single-linkage analysis (Fig. 25) shows three groups and several isolated species.

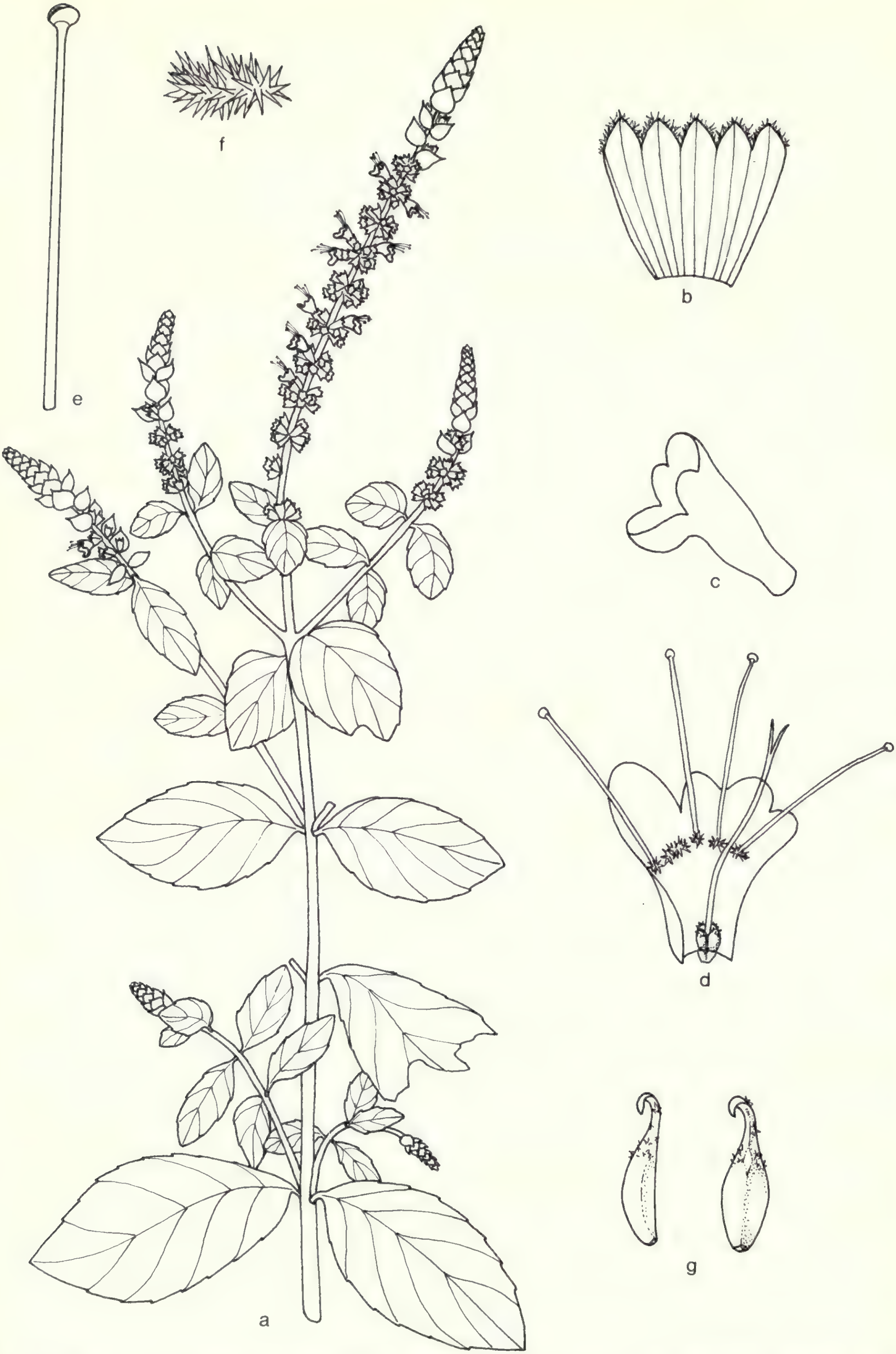

Fig. 26 *Rostrinucula dependens.* (a) habit × ½. (b) calyx × 10. (c) corolla × 5. (d) dissected flower × 5. (e) stamen × 10. (f) annular hairs at the base of a stamen filament × 40. (g) nutlet, inner face, and profile × 5.

When one group is formed it corresponds to the genus *Elsholtzia* as described by Bentham (1832–36) and other authors. When two groups are formed they correspond to section *Cyclostegia* with section *Elsholtzia* of Bentham, and section *Apahanochilus* series *Stenelasmeae* of Briquet. The section *Aphanochilus* series *Platyelasmeae* Briq. containing three species becomes divided up. Two species, *E. densa* (OTU 20) and *E. manshurica* (OTU 21), become included within the group comprised of sections *Cyclostegia* and *Elsholtzia*, and the third species, *E. eriostachya* (OTU 19), becomes included with the group comprised of section *Aphanochilus* series *Stenelasmeae.* When three groups are formed they correspond to sections *Cyclostegia* and *Elsholtzia* Benth., section *Aphanochilus* series *Platyelasmeae* Briq., and section *Aphanochilus* series *Stenelasmeae* Briq.

Elsholtzia sections Cyclostegia and Elsholtzia

The group corresponding to Bentham's *Elsholtzia* sections *Cyclostegia* and *Elsholtzia* appears as a single close-knit group in every analysis. Even *E. densa* (OTU 20) and *E. manshurica* (OTU 21) are sometimes included within this group as in the clustering to maximize WGMS analysis (see Table 6, Appendix 4).

Bentham (1829) described two genera, *Aphanochilus* and *Cyclostegia*, which he later reduced to sections of the genus *Elsholtzia*, distinguishing the sections on the basis of variation in bract and inflorescence characters. Section *Aphanochilus* has equal spikes with lanceolate or ovate bracts or secund spikes with lanceolate bracts. Section *Cyclostegia* has dense spikes and connate, imbricate, cyathiform, membranous, veined bracts with ciliate margins. Section *Elsholtzia* has broadly ovate spikes and broadly ovate, secund bracts. These sections were accepted by all subsequent authors with the exception of Kudo (1929), who reverted to Bentham's original concept of *Aphanochilus* and *Elsholtzia* as separate genera. Kudo assigned to *Elsholtzia* two species of formerly unknown sectional affinities, *E. heterophylla* (OTU 16) and *E. luteola* (OTU 14) (Fig. 27). These were later assigned to section *Cyclostegia* by Wu & Huang (1974). However, the type species of section *Cyclostegia, E. strobilifera* (Benth.) Benth. (OTU 17), was not included in Kudo's work and he did not make clear whether or not he considered *Cyclostegia* and *Elsholtzia* to be con-sectional. Several new species were assigned to both sections by Wu & Huang (1974), but the sectional definitions remained those of Bentham (1832–36). There seems to be no reason for recognizing two sections since in all of my analyses sections *Cyclostegia* and *Elsholtzia* form a single, close-knit group. Table 10 shows Bentham's characters scored for all the species of sections *Cyclostegia* and *Elsholtzia*. All species have more or less dense inflorescences and imbricate, ciliate bracts. All species have veined bracts, although in *E. concinna* (OTU 8) and *E. kachinensis* (OTU 10), which have green, non-membranous bracts, the veins are less obvious than in other species which have membranous and often brown bracts. *E. concinna* and *E. kachinensis* (Fig. 4) are the only species with non-membranous bracts. Four combinations of the remaining three characters are represented:

(1) Bracts free, non-cyathiform, inflorescence cylindrical: *E. concinna* (OTU 8), *E. hunanensis* (OTU 18), *E. kachinensis* (OTU 10).
(2) Bracts free, non-cyathiform, inflorescence secund: *E. argyi* Léveillé (OTU 13), *E. ciliata* (OTU 9), *'E. elegans'* (OTU 4), *E. feddei* Léveillé (OTU 3), *E. nipponica* Ohwi (OTU 6), *E. oldhamii* Hemsley (OTU 7), *E. pseudocristata* Léveillé & Vaniot (OTU 5), *E. pygmaea* (OTU 11), *E. soulei* Léveillé (OTU 12).
(3) Bracts connate, non-cyathiform, inflorescence secund: *E. luteola* (OTU 14).
(4) Bracts connate, cyathiform, inflorescence cylindrical: *E. bodinieri* (OTU 15), *E. heterophylla* (OTU 16), *E. strobilifera* (OTU 17).

Whichever combination of these three characters is used to divide the species into groups there is always some degree of overlap, and at least one species, *E. concinna, E. hunanensis, E. kachinensis* or *E. luteola,* will be an intermediate between the groups.

Since four of Bentham's characters, i.e. bracts dense, bracts imbricate, bracts veined, and bracts with ciliate margins have proved to be identical throughout both sections (Table 10) and the other characters, in any combination, always show intermediate species, the original

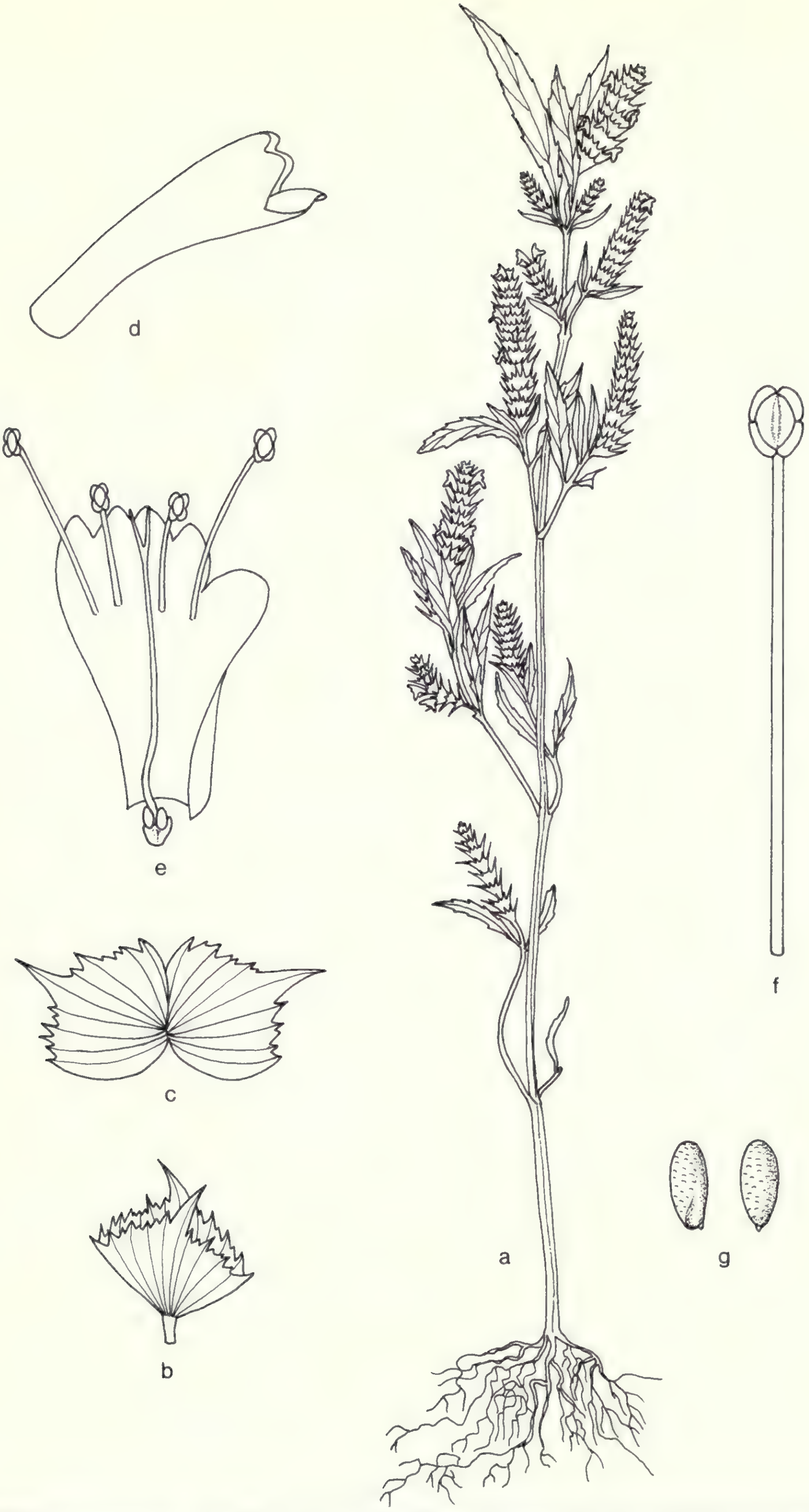

Fig. 27 *Elsholtzia luteola.* (a) habit × 1. (b) pair of fused bracts × 5. (c) pair of bracts opened out × 5. (d) corolla × 10. (e) dissected flower × 10. (f) stamen × 20. (g) nutlet, inner face, and profile × 10.

distinction between the two sections is no longer valid. My data has produced no other evidence for a division of these species into two or more higher taxa. Therefore, I have placed all 14 species in a single group, *Elsholtzia* section *Elsholtzia,* which is characterized by orbicular, membranous bracts (except in *E. concinna* and *E. kachinensis*); the inflorescence may be cylindrical, strobilate or secund but always with imbricate bracts (see p. 69).

Table 10 Bract characters in *Elsholtzia* sections *Cyclostegia* and *Elsholtzia.*

	Species	Characters							
		1	2	3	4	5	6	7	8
section *Elsholtzia*	*E. concinna*	+	+	+	+	−	−	−	−
	E. kachinensis	+	+	+	+	−	−	−	−
	E. hunanensis	+	+	+	+	+	−	−	−
	E. feddei	+	+	+	+	+	−	−	+
	'E. elegans'	+	+	+	+	+	−	−	+
	E. pseudocristata	+	+	+	+	+	−	−	+
	E. nipponica	+	+	+	+	+	−	−	+
	E. oldhamii	+	+	+	+	+	−	−	+
	E. ciliata	+	+	+	+	+	−	−	+
	E. pygmaea	+	+	+	+	+	−	−	+
	E. soulei	+	+	+	+	+	−	−	+
	E. argyi	+	+	+	+	+	−	−	+
	E. luteola	+	+	+	+	+	+	−	+
section *Cyclostegia*	*E. bodinieri*	+	+	+	+	+	+	+	−
	E. heterophylla	+	+	+	+	+	+	+	−
	E. strobilifera	+	+	+	+	+	+	+	−

Key to the characters:
1 dense +/lax −.
2 imbricate +/not overlapping −.
3 clearly veined +/obscurely veined −.
4 margins ciliate +/margins glabrous −.
5 membranous +/non-membranous −.
6 connate +/free −.
7 cyathiform +/not cyathiform −.
8 secund +/cylindrical −.
(See also Figs 4 & 27.)

Elsholtzia section Aphanochilus series Stenelasmeae

The group corresponding to Briquet's *Elsholtzia* section *Aphanochilus* series *Stenelasmeae* also appears to remain distinctive in each analysis, even though *E. eriostachya* (OTU 19) of series *Platyelasmeae* is sometimes included within it as, for example, in the clustering to maximize WGMS analysis (see Table 6, Appendix 4). Section *Aphanochilus* series *Stenelasmeae* is less well-defined than either section *Aphanochilus* series *Platyelasmeae* or section *Elsholtzia sensu mihi.* Some OTUs, e.g. *E. alopecuroides* Léveillé & Vaniot (OTU 32), *E. communis* (Collet & Hemsley) Diels (OTU 31), '*E. glanduligera*' (OTU 34) and *E. griffithii* Hook. f. (OTU 33) share high similarities with all the other OTUs in the group. Others, e.g. *E. flava* (OTU 28) and *E. fruticosa* (OTU 29), share high similarities with only a few other OTUs in the group. In the clustering to maximize WGMS analysis section *Aphanochilus* series *Stenelasmeae* seems to suffer more from the 'rag-bag' effect than any other group; loosely associated species such as *Elsholtzia integrifolia* (OTU 23) and *Eurysolen gracilis* (OTU 1) are included in the group together with the species of section *Aphanochilus* series *Stenelasmeae* simply because every species in the analysis must be placed in a group. The principal co-ordinates analysis (Figs 14–19) groups section *Aphanochilus* series *Stenelasmeae* within a large, open portion of the main species cluster.

Despite the associated species in the clustering to maximize WGMS analysis and the spreading cluster in the principal co-ordinates analysis, section *Aphanochilus* series *Stenelasmeae* is a consistently distinguishable group. Bentham (1829) and Kudo (1929) considered *Aphanochilus* to be a genus distinct from *Elsholtzia*, although Bentham qualified his view with the statement 'perhaps my *Aphanochilus* might be united with it (*Elsholtzia*) as a second section' and later he (1832–36) did just that. Kudo (1929) recognized *Aphanochilus* by the verticillate, often long and lax flower spikes, the lanceolate or sublanceolate bracts, the divergent, ultimately confluent anther locules, the equal disc, and the shining nutlets. He distinguished *Elsholtzia* (in which he included some species of Bentham's section *Cyclostegia* and Briquet's section *Aphanochilus* series *Platyelasmeae*) from it by the many-flowered verticil in secund spikes, the broadly ovate, densely imbricate bracts, the emarginate upper lip of the corolla, the lower pair of stamens longer than the upper, the divergent anther-locules, and the disc with a swollen nectary. However, in all species of *Aphanochilus* and *Elsholtzia sensu* Kudo the upper lip of the corolla is emarginate, the lower pair of stamens is longer than the upper, the anthers are bilocular, the anther locules are partially fused, and the disc has a swollen gland or nectary. Species in both genera may have long, dense, secund flower spikes. Thus, the only credible distinguishing character for separating them is the lanceolate or subulate bracts versus the broadly ovate and densely imbricate bracts.

Bentham (1829) similarly distinguished *Aphanochilus, Elsholtzia*, and a third genus *Cyclostegia* by inflorescence, bract, corolla, and anther characters. Later Bentham (1832–36) reassessed these characters and commented that 'The three sections of *Elsholtzia* differ, in many respects, from each other in habit; but on closer examination of their characters, these distinctions do not appear to be of sufficient importance to preserve the genera *Aphanochilus* and *Cyclostegia*, which I had originally established, but which I have now considered as mere sections of *Elsholtzia*.' Bentham characterized sections *Aphanochilus* and *Elsholtzia* as follows:

section *Aphanochilus*. Spikes equal, bracts lanceolate to ovate or secund with bracts lanceolate.
section *Elsholtzia*. Spikes and bracts broadly ovate, secund.

The characters match the unique characters used by Kudo (1929). Bentham's reassessment corresponds with the results presented here although, as discussed above, section *Cyclostegia* cannot be differentiated from section *Elsholtzia*, and section *Aphanochilus* series *Stenelasmeae* Briquet, rather than section *Aphanochilus sensu lato*, forms a subgroup within *Elsholtzia* to correspond with Bentham's 'mere section'.

Section *Aphanochilus* series *Stenelasmeae* was first described by Briquet (1897); the bracts were described as small, linear-lanceolate or stiffly pointed, and the nutlets shiny. Briquet created the series to differentiate the majority of the species in section *Aphanochilus* from *E. densa* and *E. eriostachya* which he placed in section *Aphanochilus* series *Platyelasmeae*, a series characterized by very short, broadly ovate or rounded bracts, and dark, dull nutlets. The group shown in my analyses corresponds almost exactly to Briquet's concept of section *Aphanochilus* series *Stenelasmeae* (although it contains several species unknown to Briquet) and is comparable to the group formed by sections *Cyclostegia* and *Elsholtzia*. Since section *Elsholtzia sensu mihi* is regarded here as a section, section *Aphanochilus* series *Stenelasmeae* has been raised to the rank of section (see p. 69). The distinguishing features of section *Aphanochilus sensu stricto* given by Briquet are rather slight. Bentham's description, although referring to section *Aphanochilus sensu lato,* provides a more suitable basis for characterizing section *Aphanochilus sensu stricto*.

In order to accommodate some newer species of *Elsholtzia* Wu & Huang (1974) described eight new series within their section *Aphanochilus* subsection *Stenelasmeae*. However, these were confined to Chinese species and although the isolated positions of *E. flava* (OTU 28) and *E. penduliflora* (OTU 25) in separate series agree with the positions shown in my analyses, on the whole their divisions are not supported by my results. Only three of Wu's & Huang's series, *Blandae, Communes,* and *Fruticosae*, contain more than one species. Series *Communes* does emerge as a fairly clear group in the single-linkage dendrogram (Fig. 25), but the other two series are not evident in the analyses. In fact, series *Fruticosae* appears as a heterogenous group, five of the six species sharing their highest similarities with species in other series, e.g. *E. winitiana*

Craib. (OTU 36), in series *Fruticosae,* with *E. blanda* (Wallich ex Benth.) Benth. (OTU 38) in series *Blandae* (see Appendix 3). In other words characters given by the authors inadequately differentiate the series. As an example, series *Capituligerae* is described as: *'frutices parvi; spicae sphaeroideae; corolla 4-fida, labio superiore integra'*. The entire upper lip of the corolla is incorrectly observed; all species of *Elsholtzia,* including *E. capituligera* (OTU 42), have an emarginate upper lip. All species have a 4-fid corolla, not just those of this series. Similarly, series *Communes* is described as: *'herbae erectae; spicae cylindriceae compactae; corolla 4-fida, labio superiore integro'*. Again the description of the upper lip is incorrect and the 4-fid corolla is common to all species in the genus. Cylindrical, compact flower spikes are also found in many species in other series e.g. *E. pilosa* of series *Pilosae*, and *E. winitiana* of series *Fruticosae.*

Elsholtzia section Aphanochilus series Platyelasmeae

The most problematical group in the analyses corresponds to Briquet's section *Aphanochilus* series *Platyelasmeae* of *Elsholtzia* which contains three species: *E. densa* (OTU 20, Fig. 28), *E. eriostachya* (OTU 19), and *E. manshurica* (OTU 21). It is only seen clearly in the single-linkage analysis (Fig. 25). The nearest neighbours list (Appendix 3) shows that *E. manshurica* shares a number of high similarities with species in section *Elsholtzia sensu mihi. E. densa* shares high similarities with *'E. elegans'* (OTU 4) of section *Elsholtzia sensu mihi* and with *'E. glanduligera'* (OTU 34) of section *Aphanochilus sensu stricto. E. eriostachya* does not share high similarities with any species from section *Elsholtzia sensu mihi.* In the clustering to maximize WGMS (Tables 5, 6, Appendix 4) and the principal co-ordinates analysis (Figs 19–21) series *Platyelasmeae* does not form a separate group. *E. eriostachya* is included in section *Aphanochilus sensu stricto*, while *E. densa* and *E. manshurica* are included in section *Elsholtzia sensu mihi.*

If *E. densa* and *E. manshurica* are considered in isolation from *E. eriostachya* then on the basis of overall similarity they could acceptably be placed in section *Elsholtzia sensu mihi*. Similarly, if *E. eriostachya* is compared only with sections *Elsholtzia sensu mihi* and *Aphanochilus sensu stricto* then it would be placed in section *Aphanochilus sensu stricto*. This is exactly the treatment given in some earlier works. Bentham (1832–36) placed *E. eriostachya* (and later, in 1848, *E. densa*) in his section *Aphanochilus* since, although the bracts were broad, like those of his section *Elsholtzia*, the inflorescence was not secund. Kudo (1929) placed *E. densa* (as *E. janthina* Dunn) in *Elsholtzia,* which he regarded as a genus in the narrow sense, although he described the inflorescence of *Elsholtzia pro majore* as secund and that of *E. densa* (Fig. 28) cylindrical.

However, *E. densa* and *E. eriostachya* are much more similar to each other than they are to any of the species of either section *Elsholtzia sensu auct.* or *Aphanochilus sensu stricto*. This is quite clear from the nearest neighbours list (Appendix 3) as well as the single-linkage analysis (Fig. 25) in which these three species form a distinct group. This view is similar to that of Briquet (1897) who placed *E. densa* and *E. eriostachya* in a separate group characterized by having short, broadly ovate or rounded bracts, and dark, matt nutlets. He considered section *Aphanochilus* series *Platyelasmeae* to merit only the rank of series, apparently on negative evidence; although series *Platyelasmeae* has broad bracts, these are neither secund as in section *Elsholtzia* nor connate as in section *Cyclostegia*. In fact, series *Platyelasmeae* seems to be intermediate between section *Aphanochilus sensu stricto* and section *Elsholtzia sensu mihi.* Table 11 gives a comparison of the bract characters in each group. Species of section *Aphanochilus sensu stricto* generally have narrow, non-membranous, non-imbricate, and usually green bracts. Species of section *Elsholtzia sensu mihi* generally have orbicular, membranous, imbricate, and usually brown or bi-coloured bracts. Species of series *Platyelasmeae* have orbicular, non-membranous, non-imbricate, and usually bicoloured or brownish bracts. In addition *E. densa, E. eriostachya,* and *E. manshurica* resemble section *Elsholtzia sensu mihi* in lacking bracteoles, which are found throughout section *Aphanochilus sensu stricto*.

Elsholtzia series *Platyelasmeae* has three distinctive characters: the fruiting calyx becomes greatly inflated (Fig. 6), the style lobes have clavate tips (Fig. 9), and the mature nutlets are distinctly verrucose (Fig. 10). *E. densa, E. eriostachya,* and *E. manshurica* are almost exactly similar to one another with respect to their qualitative character states. They differ significantly

Table 11 Bract characters in *Elsholtzia*.

sect. *Aphanochilus sensu stricto*	ser. *Platyelasmeae* Briq.	sect. *Elsholtzia sensu mihi*
not as broad as long	at least as broad as long	at least as broad as long
non-membranous	non-membranous	membranous (except for *E. concinna* and *E. kachinensis*)
non-imbricate	non-imbricate	imbricate
usually green	usually brown or bicoloured	usually brown or bicoloured (except for *E. concinna* and *E. kachinensis*)

(See also Figs 4, 27, & 28.)

only in the variation of ten quantitative characters. These were scored as simple measurements and not converted into proportions. Consequently, there is the possibility of distorted separation, particularly in the principal co-ordinates analyses, due to the size factors. This would explain the grouping of *E. eriostachya* with the generally small flowered species of section *Aphanochilus sensu stricto,* and the larger flowered *E. densa* and *E. manshurica* with section *Elsholtzia sensu mihi.*

The calyx, style, and nutlet characters were utilized by Kitagawa (1935) who recognized *Platyelasma* as a genus distinct from *Aphanochilus* and *Elsholtzia*. Table 12 gives mean group similarities for section *Elsholtzia sensu mihi,* section *Aphanochilus sensu stricto,* and series *Platyelasmeae*. The similarities support Kitagawa's recognition of *Platyelasma* as a separate taxon at the same rank as *Aphanochilus* and *Elsholtzia*. However the high similarities shared by all three groups precludes recognition of *Platyelasma* at the generic level. Despite the distribution of *E. densa, E. eriostachya,* and *E. manshurica* in the principal co-ordinates and clustering to maximize WGMS analyses, the most suitable treatment for these species is to place them in a third section: *Elsholtzia* section *Platyelasma.*

It is interesting to note here the monotypic genus *Paulseniella* described by Briquet (1908) from a plant collected in the Pamir. It has a campanulate calyx, becoming inflated in fruit, a barely exserted subequally five-lobed corolla, style lobes with globular swellings at the tips, and tuberculate-rugose nutlets. *P. pamirensis* was later recognized by Fedschenko (1908) as being based on a specimen of *Elsholtzia densa.* Although mistaking the identity of the plant, Briquet thought it sufficiently distinct to warrant its recognition as a new genus.

Table 12 WGMS and BGMS values for the subgeneric divisions of *Elsholtzia.*

1	83·6		
2	78·4	88·1	
3	78·9	75·2	87·5
	1	2	3

Key to groups:
1—section *Elsholtzia mihi.*
2—section *Aphanochilus sensu stricto.*
3—series *Platyelasmeae.*

Relocated OTUs

A number of specie of *Elsholtzia* appear to be somewhat divorced from the bulk of the genus, especially in the single-linkage analysis (Fig. 25). In almost every case the data were obtained from a single specimen and the resulting distortion appears to have affected the placing of some

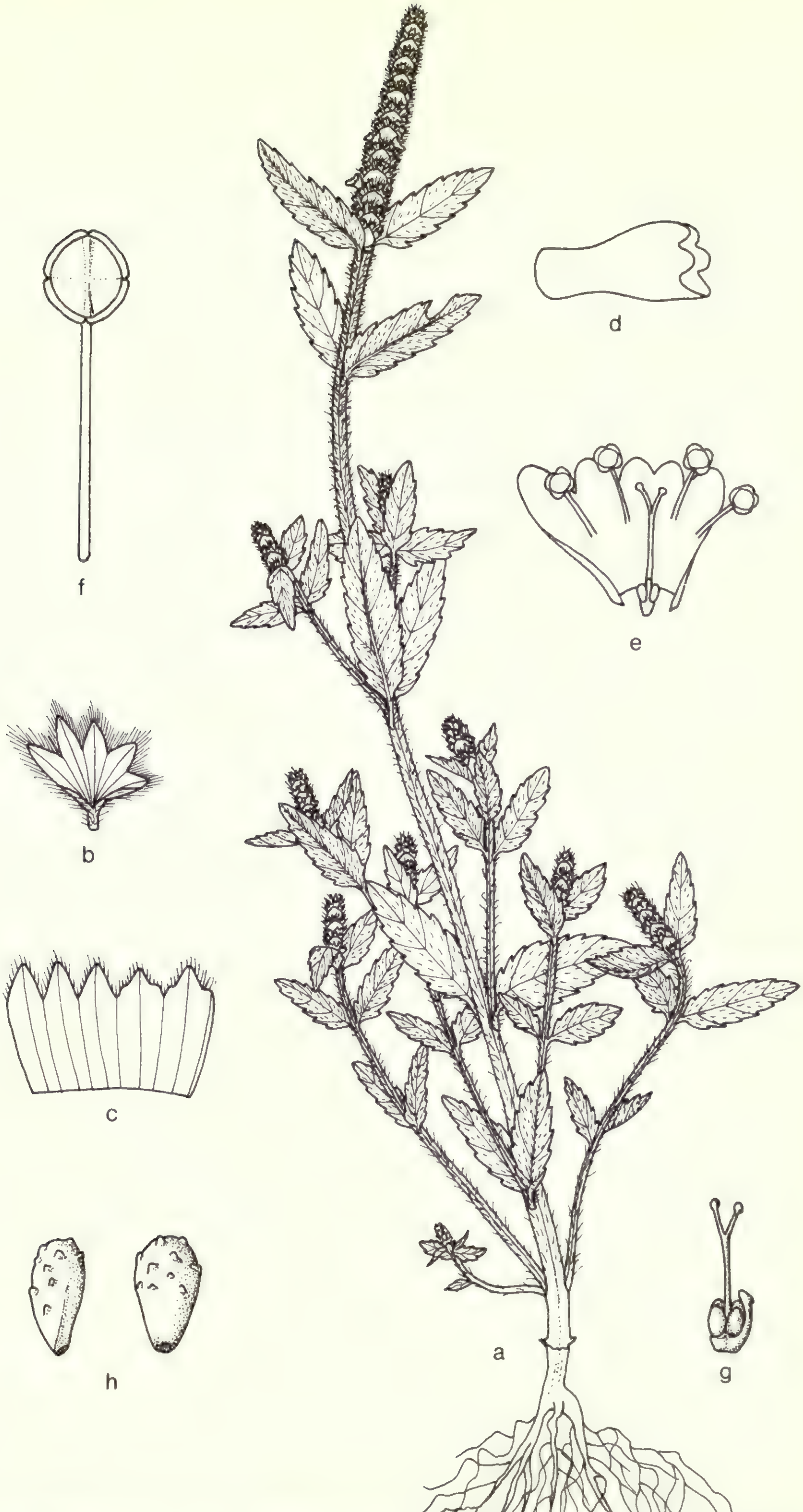

Fig. 28 *Elsholtzia densa.* (a) habit × 1. (b) calyx at anthesis × 10. (c) calyx in fruit × 5. (d) corolla × 10. (e) dissected flower × 10. (f) stamen × 40. (g) style, disc, and young nutlets × 10. (h) nutlet, inner face, and profile × 5.

species. However, most can be accurately placed by referring to the nearest neighbours list (Appendix 3).

Elsholtzia beddomei and E. kachinensis

Elsholtzia beddomei C. B. Clarke ex Hook.f. (OTU 24) and *E. kachinensis* (OTU 10) link at low similarities in the single-linkage analysis (Fig. 25). Although sharing few high similarities with other species of *Elsholtzia* there is no doubt as to where their phenetic affinities lie. Reference to the nearest neighbours list (Appendix 3) confirms that *E. beddomei* belongs to section *Aphanochilus sensu stricto,* and *E. kachinensis* to section *Elsholtzia sensu mihi.*

Elsholtzia penduliflora

Elsholtzia penduliflora (OTU 25) links at a low similarity in the single-linkage analysis (Fig. 25) and seems to be isolated from other species of *Elsholtzia.* It is rather surprising to find *Pogostemon brevicorollus* Y. Z. Sun (OTU 105) as the nearest neighbour to *Elsholtzia penduliflora* (Appendix 3). However, the data set for *Pogostemon brevicorollus* is incomplete and the similarity between it and *Elsholtzia penduliflora* may be considered as dubious. The similarity values shared by *E. penduliflora* with its remaining four nearest neighbours, *E. elata* Zoll. & Mor. (OTU 35), and *E. blanda* (OTU 38), *Pogostemon travancoricus* (OTU 92), and *P. amarantoides* (OTU 80) give no conclusive pointer to where the phenetic affinities of *Elsholtzia penduliflora* lie. Both the principal co-ordinates (Figs 14–17) and the clustering to maximize WGMS analysis (Appendix 4, Table 6) place it in *Elsholtzia* section *Aphanochilus sensu stricto.*

Elsholtzia flava, E. fruticosa and E. hunanensis

In the single-linkage dendrogram (Fig. 25), *Elsholtzia flava* (OTU 28), *E. fruticosa* (OTU 29) and *E. hunanensis* (OTU 18) are not referable to any section of *Elsholtzia.* As with the previous species the nearest neighbours list (Appendix 3) can be used to locate all three species. *E. hunanensis* belongs to section *Elsholtzia sensu mihi,* and *E. fruticosa* and *E. flava* to section *Aphanochilus sensu stricto.* However *E. flava* warrants further investigation. In this species the style is not always obviously gynobasic (see p. 22) and the nutlets have a small but laterally displaced attachment-scar (Fig. 10 and see p. 46). The bracts are unusually broad for section *Aphanochilus sensu stricto* and the very large, broadly-ovate leaves, and coarse habit help to identify this species. Should the style and nutlet-attachment characters prove to have greater value than they have been accorded here (see discussion of these characters in *Leucosceptrum,* pp. 46–47) the position of *E. flava* will need to be re-examined.

Elsholtzia concinna

Elsholtzia concinna (OTU 8) presents a more difficult situation and the evidence from the various analyses is conflicting. In the principal co-ordinates analysis (Figs 17–19) *E. concinna* might be included within either section *Aphanochilus sensu stricto* or section *Elsholtzia sensu mihi.* In the clustering to maximize WGMS (Appendix 4, Table 6) it is grouped with section *Aphanochilus sensu stricto.* In the single-linkage dendrogram (Fig. 25) it links on at the 86% level and is not referable to any section, although the nearest neighbours list (Appendix 3) shows it to be most similar to *Dysophylla mairei* (= *Elsholtzia pilosa* see pp. 57) which is a member of section *Aphanochilus.* The raw data were obtained from two rather poor specimens and should perhaps be regarded with some suspicion. Vautier (1959), when describing *E. concinna* (Fig. 4), stated that, although differing in bract and inflorescence characters, *E. concinna* and *E. strobilifera* (OTU 17) were similar in general appearance; *E. concinna* and *E. ciliata* (OTU 11) differed in leaf and inflorescence features. The clear implication was that *E. concinna* belonged to section *Elsholtzia sensu mihi. E. concinna* certainly shares the characters which define this section (Table 11) rather than those which define section *Aphanochilus sensu stricto,* although it in fact resembles *E. ciliata* more than *E. strobilifera.* In view of this, I have placed *E. concinna* in section *Elsholtzia sensu mihi* but the availability of more study material may necessitate reconsideration of its position.

Leucosceptrum plectranthoideum

Leucosceptrum plectranthoideum (OTU 128) is placed in *Elsholtzia* section *Apanochilus sensu stricto* in all the analyses except the single-linkage dendrogram (Fig. 25), where it links with *Elsholtzia,* but is not referable to any particular section.

Oringally described by Léveillé (1915–16) as *Buddleja plectranthoidea* it was transferred to *Leucosceptrum* by Marquand (1930). The type is a specimen of *Elsholtzia fruticosa* (OTU 29). *E. fruticosa* and *Leucosceptrum plectranthoideum* are not, as might be expected, inseparable, or at least very close, units in the analyses. Once again this seems due to inadequate sample size, only the type of *Leucosceptrum plectranthoideum* being available. This specimen did not fall completely within the variation range of *Elsholtzia fruticosa* as represented by the specimens used to generate the averaged data set (see p. 8).

Dysophylla mairei

Dysophylla mairei (OTU 65) was described by Léveillé (1912) as a species of *Dysophylla.* However all of the analyses clearly show it to belong to *Elsholtzia* and not to *Dysophylla.* Dunn (1915) gave *Dysophylla mairei* as a synonym of *Elsholtzia pilosa* and the type specimens compare very closely. I have accepted Dunn's view.

Elsholtzia integrifolia

All previous authors who have considered *E. integrifolia* (OTU 23) place it in *Elsholtzia* section *Aphanochilus,* thus agreeing with Bentham's original concept (1832–36). None of them appears to have seen the type specimen, a sheet only recently relocated by me at BM. As a supposed member of *Elsholtzia* section *Aphanochilus, E. integrifolia* was included in this study, but the analyses show it to be an isolated taxon, sharing an overall similarity of only 84·1% with its nearest neighbour, *E. griffithii* (OTU 33) (Appendix 3).

Wu & Huang (1977) cite *E. integrifolia* as a synonym for *Schizonepeta tenuifolia* (L.) Briq. of the tribe Nepetae, apparently on evidence obtained from a photograph. When this work became available to me in 1979, after completion of the computor runs, I compared the type of *E. integrifolia* with available material and descriptions of *Schizonepeta,* although unfortunately not of *Schizonepeta tenuifolia. Elsholtzia integrifolia* does share a greater overall similarity to other species of *Schizonepeta* than to species of *Elsholtzia*, and therefore I exclude *Elsholtzia integrifolia* from the Pogostemoneae.

'Elsholtzia japonica'

'Elsholtzia japonica' (OTU 2) was thought to be a previously undescribed species represented by two specimens in the Léveillé herbarium at E. Both specimens were collected by d'Argy in the Kiangsu province of China, and were labelled *'E. japonica'*. In the clustering to maximize WGMS (Appendix 4, Tables 5, 6) and the principal co-ordinates analyses (Figs 14–17) *'E. japonica'* clusters with *Elsholtzia.* In the single-linkage analysis (Fig. 25) it clusters with *Pogostemon.* However, *'E. japonica'* lacks certain constant features possessed by species of *Elsholtzia* and *Pogostemon.* The corolla of *Pogostemon* has an entire upper lip, also hairy stamen-filaments and unilocular anthers. *'E. japonica'* has an emarginate upper lip to the corolla, naked stamen-filaments, and bilocular anthers. *Elsholtzia* has bilocular-fused anthers and a tumescent lobe on the disc. *'E. japonica'* has bilocular-free anthers and no lobe on the disc. It also has hairy nutlets while those of *Elsholtzia* and *Pogostemon* are invariably glabrous. These characters suggest that *'E. japonica'* might be misplaced and a brief survey of genera outside the Pogostemoneae confirms that *'E. japonica'* is more similar to species of *Agastache* Clayton ex Gronovius (tribe Nepetae) and, in particular, to *A. rugosus* Fish. & Mey, to which it might belong. I have therefore excluded it from the Pogostemoneae.

The geographical distribution of *Elsholtzia* as accepted by other authors was rather striking. Most species occur in eastern Asia and Malesia with the weedy species, *E. ciliata* (OTU 9), extending over a wider area as far as central Europe (where it may be a relict of cultivation). A single, very isolated species, *E. aquatica* (OTU 22), occurs in southern Malawi. However, the transfer of this species to *Pogostemon* rectifies the disjunction.

Keiskea

The five species of *Keiskea* form a discrete and homogeneous group in all the analyses. They are most similar to species of *Elsholtzia* and share slightly higher similarities with species of section *Elsholtzia sensu mihi* than with the other sections. This confirms the view of earlier authors (e.g. Bentham & Hooker, 1876; Ohwi, 1965) who placed *Keiskea* next to *Elsholtzia*. The two genera were said to differ mainly in features of the calyx, that of *Keiskea* being deeply divided and sometimes described as bilabiate, while that of *Elsholtzia* is shallowly toothed and not bilabiate. During this study, several other characters which distinguish the genera have been determined. As well as being deeply divided, the calyx in *Keiskea* (Fig. 6) has an annulus of hairs in the throat. No *Elsholtzia* possesses such an annulus. Similarly, *Keiskea* (Fig. 7) has a complete annulus of hairs within the corolla. Some species of *Elsholtzia*, e.g. *E. rugulosa* (OTU 26) (Fig. 7), also possess an annulus within the corolla but these annuli are always incomplete, with the ends of the open circle of hairs extending dorsally under the upper lip.

In *Elsholtzia* the number of mature nutlets is always four. Fertilized flowers of all species of *Keiskea* have four very young nutlets but at maturity *Keiskea japonica* (OTU 132), the only species in which mature nutlets are known to me, has only one (Fig. 10), a character also noted by Ohwi (1965). However my sample was very small and the abortion of one, two or three nutlets is common in Labiatae. It may be that a larger sample will show the normal number of mature nutlets in *Keiskea* to be four.

The confluence of the anther locules is a variable character. *Keiskea* has bilocular anthers in which the locules are free and separated by a short connective. *Elsholtzia* has bilocular anthers in which the locules are confluent, although still recognizably bilocular (Figs 8, 27). The single exception to this is *E. hunanensis* (OTU 18) which has anthers similar to those of species of *Keiskea*. Thus, although this appears to be a distinguishing feature between the two genera, the exceptional *Elsholtzia* species show it to be a linking character too.

A clear phenetic similarity of *Keiskea* with *Elsholtzia* is established by a number of other characters. The shared characters of a (sometimes weakly) bilabiate corolla with an emarginate upper lip and spreading, three-lobed lower lip were recognized by earlier authors (Bentham & Hooker, 1876; Briquet, 1897; Ohwi, 1965). In addition both genera have a single tumescent gland on the disc (Fig. 9), a unique character within the tribe. In *Keiskea* the bracts are similar in shape and texture to those of a number of *Elsholtzia* species, e.g. *E. flava* (OTU 28) (Fig. 4). The few-flowered verticils forming a loose, secund inflorescence in *Keiskea* are also typical of some species of *Elsholtzia*, particularly those of *Elsholtzia* section *Elsholtzia sensu mihi* e.g. *E. ciliata* (OTU 9).

Only one species of *Keiskea*, *K. macrobracteata*, is omitted from this study for lack of available material. However, from the description all the comments made above equally apply. Its description suggests that it may be the most similar species to the taxa of *Elsholtzia* section *Elsholtzia sensu mihi*, particularly with respect to the bract characters. In the protologue Masamune (1940) considered that its conspicuous features distinguished it from other *Keiskea* species and divided the genus into two sections:

Section I. *Macrobracteatae*.
Bractea ovata-rotundata. Carex (sic) bi-labiatus supra barbatus. K. macrobracteata.
Section II. *Eukeiskea*.
Bracteata linearis. Carex (sic) late campanulatus extus subglaber. K. japonica K. sinensis.

However the calyx characters used to distinguish the sections are inapplicable since all the species have calyces which are bilabiate and hairy above. *K. elsholtzioides* (OTU 133) (Fig. 4) has longer, broader bracts than other species and might be placed in section *Macrobracteatae*. The bracts of the other species are narrower but could hardly be described as linear. There seems to be little support for Masamune's division, but the lack of specimens of *K. macrobracteata* prevents a complete assessment from being made.

Tetradenia

The three species of *Tetradenia,* like *Keiskea,* form an obvious group in all analyses. Again like *Keiskea, Tetradenia* is most similar to *Elsholtzia.* The clustering to maximize WGMS analysis (Table 7) suggests a greater similarity to *Elsholtzia* section *Elsholtzia sensu mihi* than to *Elsholtzia* section *Aphanochilus sensu stricto*, but this is not borne out by the principal co-ordinates analyses (Figs 14–16).

In the genus protologue Bentham (1829) recognized *Tetradenia* by the four tumescent lobes on the disc and placed it 'immediately before *Elsholtzia*'. In a later work (1832–36) he expanded this statement considerably: 'it [*Tetradenia*] is intermediate between *Elsholtzia* and *Colebrookea*: it differs from the first by the calyx and by the more regular corolla; from *Colebrookea* by the calyx not plumose at the maturity of the fruit, by the style less deeply cleft; and from both by the remarkable glands of the ovarium'.

Despite the link with *Elsholtzia,* Bentham (1848) and other authors (e.g. Bentham & Hooker, 1876) grouped *Tetradenia* with *Colebrookea, Dysophylla,* and *Pogostemon*; the group was characterized particularly by unilocular anthers or the anther locules confluent, the corolla tube rarely longer than the calyx, the lobes equal or the anterior lobes longer. *Elsholtzia* was placed in another group characterized by distant or sometimes confluent anther locules.

The evidence of this study supports a link for *Tetradenia* with *Elsholtzia* rather than with *Colebrookea, Dysophylla,* and *Pogostemon* (although from the principal co-ordinates analyses, Figs 11–13, *Colebrookea* would appear to be more similar to *Tetradenia* than are either *Dysophylla* or *Pogostemon*). The proximity of *Tetradenia* and *Elsholtzia* in all of the analyses except the single-linkage analysis (Fig. 25) is clear evidence of the phenetic similarity between the genera. This is reflected by a number of characters. Perhaps the most obvious are the shape of the corolla, the shape and texture of the bracts, the bilocular (not unilocular) anthers, and the pollen types. Both *Tetradenia* and *Elsholtzia* have emarginate upper lobes to the corolla. The corolla in most species of *Elsholtzia,* as observed by Bentham, is more markedly bilabiate than that of species of *Tetradenia,* but some species of *Elsholtzia,* e.g. *E. densa* (OTU 20) and *E. myosurus* Dunn (OTU 39) have similar corollas (Figs 7, 28). *Dysophylla* and *Pogostemon* have entire upper lips to the corolla. The link between *Tetradenia* and *Elsholtzia* section *Elsholtzia sensu mihi* is emphasized by the similarity of the bracts (Fig. 4). In both the bracts are orbicular or somewhat broader than long, usually brown (or bi-coloured) and membranous. *Elsholtzia* section *Platyelasma sensu mihi* also has broad, brown or bi-coloured bracts, but they are not membranous. Similar bracts are found in *Elsholtzia flava* (OTU 28) (Fig. 4). Like *Elsholtzia* section *Elsholtzia sensu mihi* and *Elsholtzia* section *Platyelasma sensu mihi, Tetradenia* lacks bracteoles. This contrasts markedly with *Dysophylla, Pogostemon,* and *Elsholtzia* section *Stenelasmeae sensu stricto* which all possess bracteoles. The anthers of *Tetradenia* species are bilocular and confluent through fusion, not unilocular as given by Bentham (1848) and Bentham & Hooker (1876). The pollen of *Tetradenia* is tri-nucleate and hexa-colpate, as is that of *Elsholtzia* and *Keiskea* (see Table 4). All other genera in the Pogostemoneae have bi-nucleate and tri-colpate pollen.

Two other characters that help to link *Tetradenia* with *Elsholtzia,* while divorcing it from *Colebrookea, Dysophylla,* and *Pogostemon,* are the glabrous anther filaments (all species of *Pogostemon* and *Dysophylla* have hairy anther-filaments) and tumescent glands on the disc (absent in *Colebrookea* (Fig. 9), *Dysophylla,* and *Pogostemon*). The tumescent glands provide one of two unique features for *Tetradenia* by having four bright red glands encircling the disc. The young nutlets rise above the glands (Fig. 9), but as they mature the glands enlarge greatly, finally overtopping the nutlets. A second unique feature is a calyx character. The upper tooth of the calyx is very broad, much broader than, and overlapping, the teeth on either side of it, unknown in other Pogostemoneae (Fig. 6).

The corolla in *Tetradenia* has a complete annulus of hairs within its throat (Fig. 7). Although some species of *Elsholtzia,* e.g. *E. rugulosa* (OTU 26), have annuli, they are never complete circles of hairs. Elsewhere, complete annuli are found only in *Comanthosphace* and *Keiskea.*

Eurysolen

The taxonomic position of *Eurysolen* is an open question. Prain (1898, 1901) described the only species, *E. gracilis* (OTU 1) (Fig. 29), and tentatively placed it near *Gomphostemma* Benth. in his tribe Prasieae, citing only the one-celled anther character as supporting evidence for his choice. Briquet (see Prain, 1901) suggested that *Eurysolen* might be placed in the Prasieae or the Ajugoideae. However, the lack of mature fruits prevented the exact determination of its position.

Later authors were similarly hampered by lack of fruiting material. Kudo (1929) placed *Eurysolen* in the Prasieae; Mukerjee (1940) placed *Eurysolen* in his tribe Ajugoideae. Wu (1959) placed *Eurysolen* in the Ajugoideae but noted an apparent relationship with *Pogostemon*. Unfortunately, he did not amplify this in any way. Chermsirivathana (1963) examined a number of fruiting specimens and described the mature fruits as dry and with a small basal attachment. On this evidence she placed it with *Colebrookea, Dysophylla, Elsholtzia,* and *Pogostemon* in her subfamily Stachyoideae. This was supported by Keng (1969, 1978) who considered that, in general habit, inflorescence, and flower structure *Eurysolen* was identical with another member of the Stachyoideae, *Achyrospermum* Blume.

My study is restricted to the tribe Pogostemoneae and the exact position of *Eurysolen* cannot be ascertained without reference to the other tribes to which it might belong. However if Chermsirivathana's and Keng's reasons for rejecting the Ajugoideae and Prasieae are accepted, *Eurysolen* would seem well-placed with the other genera of the Pogostemoneae. My own examination of mature fruits of *Eurysolen gracilis* (Fig. 10) confirms Chermsirivathana's observations; they are dry and not fleshy as in the Prasieae and the attachment scar is small and basal, not large and lateral as in the Ajugoideae. In general habit and inflorescence *E. gracilis* resembles some species of *Pogostemon,* e.g. *P. wightii* Benth. (OTU 100), and in floral structure resembles species of *Elsholtzia* and *Rostrinucula* (Fig. 7).

The analyses give conflicting results for the affinities of *Eurysolen gracilis* within the Pogostemoneae. It is not very similar to any other OTU, although it shares its highest similarities with species of *Elsholtzia* section *Aphanochilus sensu stricto.* Appendix 3 shows that its nearest neighbour is *Dysophylla mairei* (OTU 65) (= *Elsholtzia pilosa,* see p. 000) with the very low similarity of 81.5%. The single-linkage analysis (Fig. 25) also shows *Eurysolen gracilis* to be an OTU of rather remote affinity with other members of the tribe.

The principal co-ordinates (Figs 11–16) and clustering to maximize WGMS analyses (Tables 5–7) clearly and consistently show *Eurysolen gracilis* as a member of *Elsholtzia* section *Aphanochilus sensu stricto,* inseperable even in the principal co-ordinates analysis of the *Comanthosphace*/*Elsholtzia* subset (Figs. 14–16). The results should not perhaps be taken at face value. In the principal co-ordinates analyses the inclusion of *Eurysolen gracilis* in the *Elsholtzia* species cluster is almost certainly due to one of the flaws in this method. The axes used to produce the two-dimensional plots are those corresponding to the largest eigenvalues, i.e. those axes in the direction of maximum variance. Only the first four axes are normally used and this may be insufficient to split OTUs apart. The presence of *Eurysolen gracilis* in the *Elsholtzia* group in the clustering to maximize WGMS is probably due to the 'rag-bag' effect. Since every unit must be placed in a group and the pre-selected number of groups has already been formed at higher levels of similarity, *Eurysolen gracilis* has been placed with its nearest neighbour *Dysophylla mairei* (OTU 65). That the similarity of *Eurysolen gracilis* to *Dysophylla mairei* is very low (81·2%) does not affect the inclusion of these two OTUs in the same group; *Eurysolen gracilis* only appears to be a part of the *Elsholtzia* cluster. The single-linkage analysis (Fig. 25) suggests that this inclusion is unlikely and the nearest neighbours list confirms that they are separate taxa. The pollen data (Table 4) lends further support to the separation of *Eurysolen* and *Elsholtzia*. In all species of *Elsholtzia* examined the pollen is tri-nucleate and hexa-colpate. In *Eurysolen gracilis* the pollen is bi-nucleate and tri-colpate.

Eurysolen gracilis does share some characters with other members of the tribe, most notably an invagination of the corolla and hairy bosses at the base of the stamen filaments as in species of *Rostrinucula,* and unilocular anthers as in *Comanthosphace, Dysophylla, Pogostemon,* and *Rostrinucula.* It is distinguished within the Pogostemoneae by a combination of three charac-

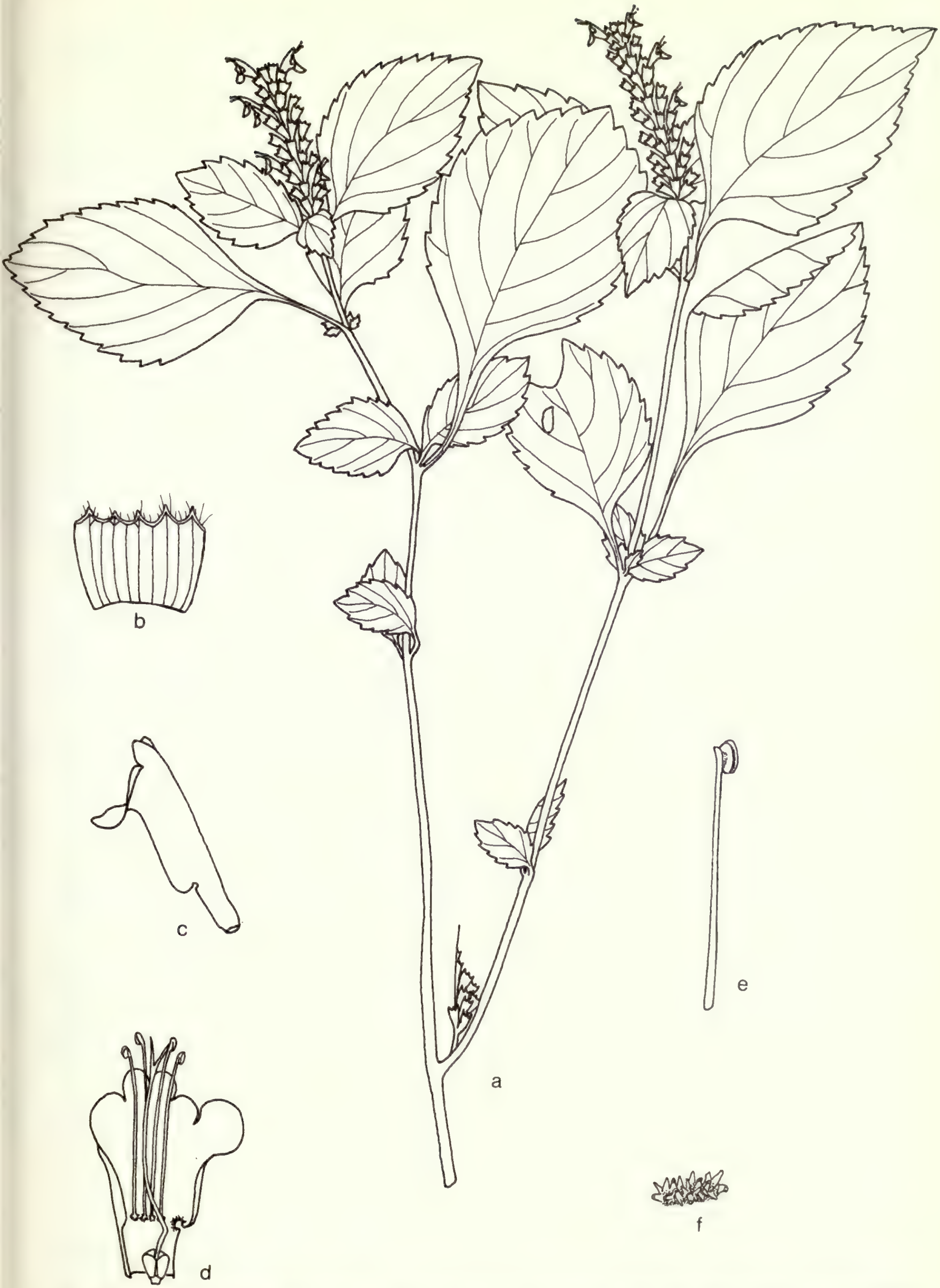

Fig. 29 *Eurysolen gracilis*. (a) habit × 1. (b) calyx × 5. (c) corolla × 5. (d) dissected flower × 5. (e) stamen × 10. (f) annular hairs at the base of a stamen filament × 40.

ters: the absence of a tumescent gland on the disc, the emarginate upper lip of the corolla, and the corolla tube gibbous towards the base (Fig. 29).

Pogostemon and ***Dysophylla***

Although usually treated as separate genera, *Dysophylla* and *Pogostemon* have been considered congeneric by several authors (Hasskårl, 1842; Miquel, 1856; Kuntze, 1891). Bentham (1870) retained the two as separate genera and commented that if they were to be regarded a single genus *Pogostemon, Dysophylla* would still be a distinct section. Keng's (1978) arrangement in which species of *Dysophylla* are confined to *Pogostemon* section *Eusteralis* (Rafin.) Keng agrees with Bentham. El-Gazzar & Watson (1967) produced a modified treatment for the two genera. On the basis of a comparison of six characters: leaf shape, leaf arrangement and indumentum, petiole length, calyx inclusions, and presence of stem aerenchyma in 22 species of *Pogostemon* (approximately 37% of the genus) and 16 species of *Dysophylla* (approximately 47% of the genus) they transferred the four species of *Dysophylla* section *Oppositifoliae* to *Pogostemon*. Their emended genera were characterized as follows:

Dysophylla. Leaves verticillate, 3–10 in a whorl, linear, sessile and usually glabrous. Corolla subequally quadrifid.
Pogostemon. Leaves opposite, ovate or narrowly ovate, petiolate, usually more or less hairy or tomentose. Corolla usually subilabiate, upper lip trifid, lower entire.

My results are in broad agreement with El-Gazzar's & Watson's view that species of *Dysophylla* section *Verticillatae* should be grouped together, while the species of section *Oppositifoliae* should be grouped with species of *Pogostemon*. However, all my analyses point to a greater degree of unity between these groups than is generally acceptable between two genera.

Although El-Gazzar & Watson's evidence and arguments are clear and persuasive, their division of the genera is based on a rather narrow sample. If the species of my wider sample are described in terms of the morphological features which characterize *Dysophylla* and *Pogostemon sensu* El-Gazzar & Watson, they form a transition series between the two extremes represented by the authors' taxa. The stages in the series are as follows:

1. Leaves in whorls of three or more, sessile, linear, truncate at the base, glabrous, corolla with upper lip equalling or shorter than lower; this describes *Dysophylla sensu stricto*; *Dysophylla stellata* (OTU 53) is typical.
2. Leaves in whorls of four, sessile, linear, truncate at the base, sparsely hairy, corolla with upper lip equalling lower; e.g. *Dysophylla linearis* (OTU 54).
3. Leaves in whorls of three or more, sessile, linear, truncate at the base, hairy, corolla with upper lip equalling lower; e.g. *Dysophylla cruciata* Benth. in Wallich (OTU 55), *D. gracilis* Dalz. in Hook.f. (OTU 62), *D. koehneana* (OTU 61), and *D. szemacensis* Y. C. Wu & Hsuan (OTU 59).
4. Leaves in whorls of three or four, very shortly petiolate, linear, attenuate at the base, densely hairy, corolla with upper lip equalling or shorter than lower; e.g. *Dysophylla falcata* (OTU 58) and *D. quadrifolia* (OTU 56). Several specimens of *D. quadrifolia* in the herbarium at E have paired leaves instead of the more usual whorls of three. The isotype of *Dysophylla falcata* (the only specimen examined) appears to have leaves in whorls of three, changing to pairs of leaves at the two uppermost nodes.
5. Leaves in whorls of three, sessile, broadly ovate to orbicular, cuneate at the base, sparsely hairy, corolla with upper lip equalling lower; e.g. '*Dysophylla trinervis*' (OTU 43) (Fig. 33).
6. Leaves in pairs, sessile, ovate, truncate at the base, densely hairy, corolla with upper lip equalling lower; e.g. *Dysophylla andersonii* Prain (OTU 66).
7. Leaves in pairs, petiolate, linear to narrowly ovate, cuneate at the base, sparsely hairy, corolla with upper lip equalling lower; e.g. *Dysophylla salicifolia* (OTU 69).
8. Leaves in pairs, shortly petiolate, ovate, cuneate at the base, glabrous, corolla with upper lip equalling lower; e.g. '*Dysophylla glabrata*' (OTU 67) (Fig. 32).
9. Leaves in pairs, shortly petiolate, ovate, cuneate at the base, hairy (sometimes densely so),

corolla with upper lip equalling lower; e.g. *Dysophylla auricularia* (OTU 68), *D. myosuroides* (OTU 71), and *D. rugosa* (OTU 70).

10. Leaves in pairs, very shortly petiolate, ovate, cuneate at the base, sparsely hairy, corolla with upper lip longer than lower; e.g. *Pogostemon strigosus* (OTU 102). This species bears a striking resemblance to *Dysophylla auricularia.*
11. Leaves in pairs, shortly petiolate to subsessile, ovate, cuneate at the base, sparsely hairy to subglabrous, corolla with upper lip longer than lower; e.g. *Pogostemon micangensis* G. Taylor (OTU 85) and *P. mutamba* (OTU 86, Fig. 30).
12. Leaves in pairs, petiolate, linear, cuneate at the base, densely hairy, corolla with upper lip equalling lower; e.g. *Pogostemon nilagiricus* (OTU 116).
13. Leaves in pairs, petiolate, ovate to orbicular, cuneate, attenuate or rounded at the base, hairy, corolla with upper lip equalling or longer than lower; *Pogostemon sensu stricto,* including e.g. *Pogostemon hirsutus* Benth. (OTU 109), *P. menthoides* (OTU 82), and *P. rupestris* Benth. (OTU 110).

On this basis *Dysophylla* and *Pogostemon* should not be retained as separate genera and the consequences of this are that Hasskårl's (1842) proposal to unite *Dysophylla* and *Pogostemon* must be accepted, and El-Gazzar's & Watson's (1967) proposal rejected. However, their thesis that *Dysophylla* section *Oppositifoliae* is much closer to *Pogostemon sensu stricto* than to *Dysophylla sensu stricto* is correct. Keng (1978) has written a classification which unites *Dysophylla* and *Pogostemon* incorporating the view of El-Gazzar & Watson. On the separation of *Dysophylla* and *Pogostemon* he stated that 'the phyllotaxis is insufficient taxonomically for a (division at the) generic level' and accepted *Pogostemon* in the widest sense, including *Dysophylla.* However, he made use of phyllotaxis to define two new sections. He accepted the joining of the opposite-leaved species of *Dysophylla* with *Pogostemon sensu stricto* to form section *Pogostemon* and placed the verticillate-leaved species of *Dysophylla* in section *Eusteralis.* Keng's conclusions were based only on studies of 10 Malesian species but his eminently sensible arrangement fits the data from my wider sample too and is followed here (see pp. 71–74). With the exception of *Dysophylla falcata* (OTU 58) and *D. quadrifolia* (OTU 56) the species are easily divided between the sections. However to accommodate these exceptional species slight modification of Keng's distinguishing characters of the sections is required:

Pogostemon section *Pogostemon.* All leaves in opposite pairs, usually petiolate, the corolla with the upper lip equalling or longer than the lower.

Pogostemon section *Eusteralis.* At least some of the leaves in whorls of three or more, usually sessile, the corolla with the upper lip equalling or shorter than the lower.

Indirect support for this treatment comes from Cook (1978) who described from several unrelated families the occurrence of a complex of characters including erect, unbranched stems with simple, elongate leaves borne in whorls which he called the '*Hippuris* syndrome'. This syndrome is found only in aquatic or amphibious plants, appearing to be developed purely as a response to habitat. Among the plants named by Cook as exhibiting the '*Hippuris* syndrome' are species of *Pogostemon* section *Eusteralis.* These species do indeed show all the required characters, including absence of hairs from most parts of the plants, stems which are creeping below, erect above, and small flowers with very short pedicels. The characters used by earlier authors (e.g. El-Gazzar & Watson, 1967) for the maintenance of *Dysophylla* as a genus distinct from *Pogostemon* are precisely those of the '*Hippuris* syndrome'.

All species of *Pogostemon* section *Eusteralis* are plants of wet habitats, while many (though by no means all) species of *Pogostemon* section *Pogostemon* are plants of stony, dry grounds or forest margins. Some species of section *Eusteralis,* e.g. *P. falcatus* (C. Y. Wu) C. Y. Wu & H. W. Li and *P. quadrifolius* (Roxb.) Kuntze, inhabit the dryer parts of wet habitats or areas prone to drying out. It is noticeable that these species sometimes possess characters which are typical of species of section *Pogostemon,* e.g. toothed, hairy, petiolate leaves borne in opposite pairs. Similarly two species of section *Pogostemon, P. micangensis* (OTU 85) and *P. mutamba* (OTU 86) (Fig. 30) which grow along watercourses in southern tropical Africa resemble species of section *Eusteralis* in their general habit, branching and very shortly petiolate leaves. Both species are normally hairy but the type specimen of *P. micangensis,* which according to the field notes was 'an aquatic herb in the marshes of the river Micango' is virtually glabrous. This evidence thus supports the union of *Dysophylla* and *Pogostemon,* since many of the characters formerly separating the genera are ecological adaptations in particular species.

Subgeneric divisions

Bentham (1832–36) divided *Pogostemon sensu stricto* into two groups § *Paniculatae* and § *Racemosae* on the basis of inflorescence structure. Briquet (1897) adopted Bentham's divisions, expanded the characters on which they were based and further subdivided each group. His characters for these groups (Table 13) do not contrast; for example § *Paniculatae* has linear-subulate bracts while § *Racemosae* has stamens which are hairy all over. If the characters defining each group are scored for the species of the other group only one character remains valid for defining them, i.e. spikes paniculately branched versus spikes simple. This character varies between specimens and in my view the variation of the inflorescence is better expressed as verticils not secund versus verticils sub-secund (see character 62 in Table 3). The clustering to maximize WGMS analysis (Table 7, Appendix 4) indicates the presence of two groups (groups five and seven) which roughly correspond to Bentham's and Briquet's groups. However, there is sufficient overlap to prevent clear definition of these groups, nor do they appear in the other analyses, and I have not formally recognized them.

Briquet's characters for defining the subdivisions A and B in each group (Table 13) do contrast but are misapplied. His *Glabriuscula* and *Barbata* in § *Racemosae* are distinguished by the stamens being naked or hairy respectively. All species of *Pogostemon* have hairy stamens, although some species, e.g. *P. travancoricus* (OTU 92) (Fig. 8), bear hairs only on the lower portions of the filaments which are not clearly visible from examination of an undissected flower. However, even if Briquet's character is substituted by the one 'filaments hairy in the lower half versus filaments hairy in the upper half' no useful division of the species can be made, since, for example *P. rotundatus* Benth. (OTU 101) with filaments hairy in the lower half would be placed in a separate group from *P. mollis* (OTU 91) with filaments hairy in the upper half, even though they share a very high overall similarity and are each other's nearest neighbour (Appendix 3). Similarly the inflorescence character used by Briquet to divide A and B in § *Paniculatae* (Table 13) does not provide a clear or useful division of the species, and I have discarded his groups.

Table 13 Names and diagnoses of Briquet's (1897: 328–329) subdivisions of *Pogostemon*.

§1. *Racemosa* Benth. Spicastra einfach, unterbrochen. Bracteen lineal-pfriemlich, kürzer als der Kelch.
  A. *Glabriuscula* Briq. Stb. mit nacten oder fast kahlen Stf.
  B. *Barbata* Briq. Stb. mit deutlich dichtbärtigen Stf.
§2. *Paniculata* Benth. Spicastra rispig verzweigt. Stb. überall mit bärtig behaarten Stf.
  A. Scheinwirtel meistens entfernt, in unterbrochenen Spicastris.
  B. Scheinwirtel meistens in dicken oder Spicastris (vergl. oben *P. suave*).

Briquet also divided *Dysophylla* into two sections, section *Rhabdocalicinae* and section *Goniocalicinae* (Table 14). Here too, there is only one contrasting character. Members of both sections have verticillate, sessile and entire leaves, and may be annual, leaving only the character calyx-tube terete versus calyx-tube strongly five-angled. The opposite-leaved species of his section *Rhabdocalicinae* are those which form Bentham's section *Oppositifoliae* and are removed to *Pogostemon sensu stricto.* As with *Pogostemon sensu stricto* the analyses show no evidence of groupings which match those of Briquet. Thus I have discarded these sections.

Relocated OTUs

Dysophylla mairei is discussed on p. 57.

Elsholtzia aquatica

All analyses group *Elsholtzia aquatica* (OTU 22) with *Pogostemon sensu lato,* and examination of the characters readily show that its inclusion in *Elsholtzia* is erroneous. It has linear, sessile,

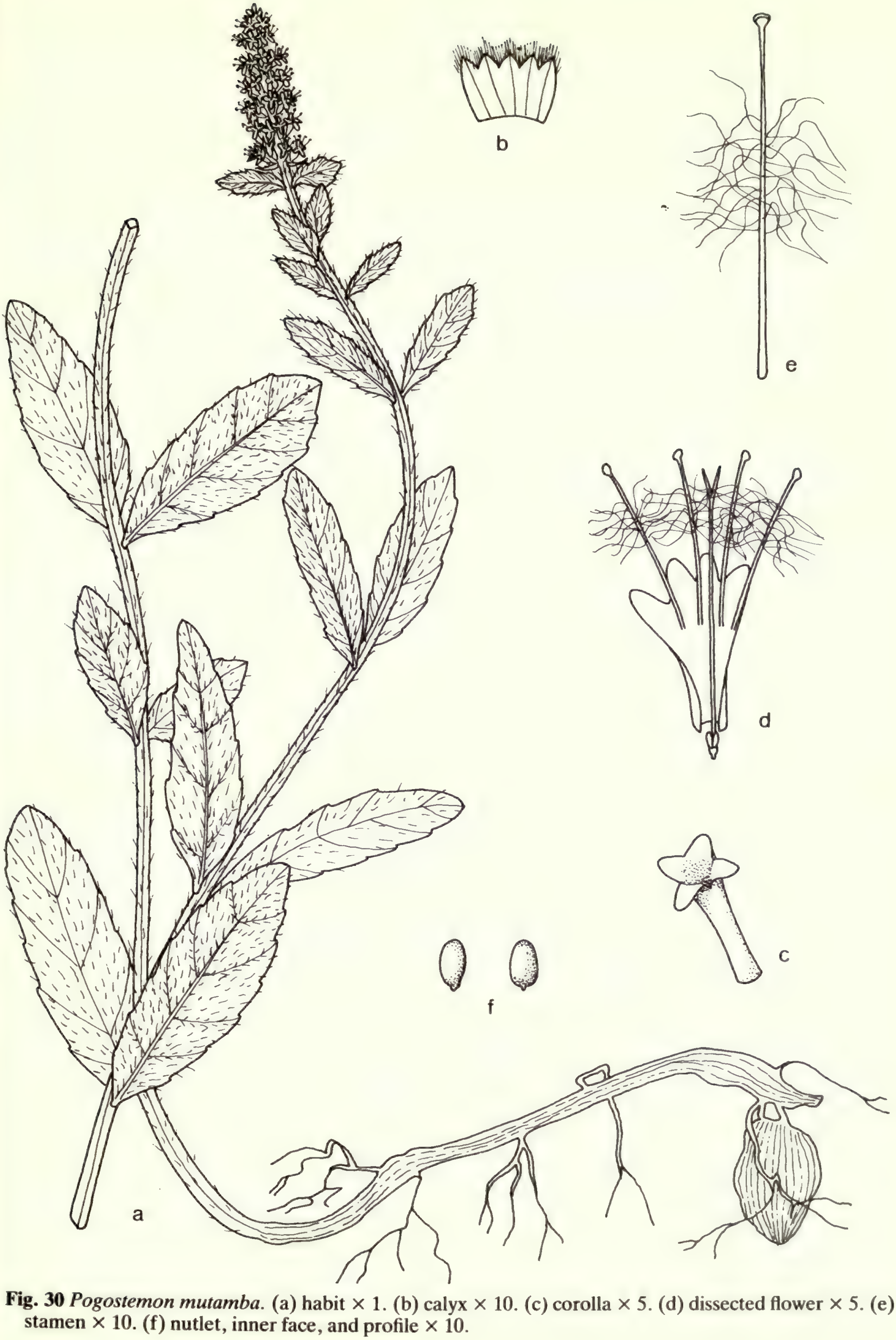

Fig. 30 *Pogostemon mutamba*. (a) habit × 1. (b) calyx × 10. (c) corolla × 5. (d) dissected flower × 5. (e) stamen × 10. (f) nutlet, inner face, and profile × 10.

verticillate leaves, an inflorescence of numerous small flowers in crowded whorls, a corolla with an entire upper lip which is shorter than the lower lip, stamens with unilocular anthers and hairy filaments, and no tumescent gland on the disc. None of these characters is shared by any species of *Elsholtzia,* but they all distinguish *Pogostemon sensu lato* and in particular *Pogostemon* section *Eusteralis*. *Elsholtzia aquatica* is thus transferred (see p. 73).

Table 14 Names and diagnoses of Briquet's (1897: 330–331) subdivisions of *Dysophylla*.

- Sect. I. *Rhabdocalicinae* Briq. Kelchröhre cylindrisch und stielrund oder sehr undeutlich, stumpf 5eckig. B. gegen-oder quirlständig, gezähnt oder ganzrandig.
  - §1. *Oppositifoliae* Benth. B. gegenständig
    - A. Ausdauernde Arten, mit meistens holziger entwickelter Wurzel oder unteriridischen Stengel.
    - B. Einjährige Art, abstehend behaart, mit sitzenden oder kurz gestielten, eilänglichen, gesägten B, behaarten Spicastris und 3eckigen, zur Fruchtzeit nach innen gebogenen Kelchzähnen.
  - §2. *Verticillatae* Benth. B. in Quirlen zu 3 oder 4 (selten bis 10).
- Sect. II. *Goniocalicinae* Briq. Kelchröhre 5kantig, mit vorspringenden Kanten. 1jährige Arten mit quirlständigen, sitzenden, ganzrandigen B.

Distribution of Pogostemon

The genus *Pogostemon* has a disjunct distribution (Fig. 31); most species are confined to the Indo-Chinese and Malesian regions and Japan with *P. stellatus* (Lour.) Kuntze extending as far as northern Australia, but three species, *P. aquaticus* (C. H. Wright) Press (OTU 22), *P. micangensis* (OTU 85), and *P. mutamba* (OTU 86) (Fig. 30) are confined to southern tropical Africa. There is no evidence for any species of *Pogostemon* occurring in the intervening areas and the nearest members of the tribe are the three species of *Tetradenia* which are found in Madagascar. The analyses do not separate the African species from the Asian and Australian species in any way and there is no morphological evidence to help explain the distribution.

Colebrookea

Colebrookea is the most isolated of all the genera within the Pogostemoneae and has no strong affinities with any of the other taxa. The nearest neighbours of *C. oppositifolia* (OTU 138) and *C. ternifolia* (OTU 137) occur in *Pogostemon* and *Elsholtzia* section *Aphanochilus sensu stricto* (Appendix 3).

Previous authors have neither discussed nor commented on the affinities and relationships of *Colebrookea* beyond placing it next to *Pogostemon* (see Bentham, 1832–36; Bentham & Hooker, 1876; Hooker, 1885; Briquet, 1897; Kudo, 1929; Wu, 1977) with which it shares the characters of unilocular anthers and an equal disc. These authors have given undue emphasis to the rather tenuous relationship between it and *Pogostemon.* While my analyses confirm this, they also show that *Colebrookea* is not significantly more similar to *Pogostemon* than it is to *Elsholtzia.* Grouping *Colebrookea* with *Pogostemon* has also tended to obscure the recognition of *Colebrookea* as a distinct genus which is so apparent in my results. Bentham (1832–36) believed *Tetradenia* to be an intermediate genus between *Colebrookea* and *Elsholtzia,* but I have found no supporting evidence for this.

Colebrookea is easily recognized by the distinctive features of the fruiting calyx, particularly the calyx teeth becoming greatly elongated and plumose (Fig. 6). The single, hairy nutlet (Fig. 10) does not fall from the calyx when ripe, but remains firmly attached to the disc, fruit and calyx acting as a diaspore. The plumose calyx teeth give the infructescence a characteristic fluffy appearance. *Colebrookea* may also be recognized by a combination of characters which are found in other genera within the Pogostemoneae. Like *Pogostemon sensu lato* it has an equal disc and unilocular anthers, but the filaments are naked (Fig. 8) and the upper lip of the corolla (Fig. 7) is emarginate.

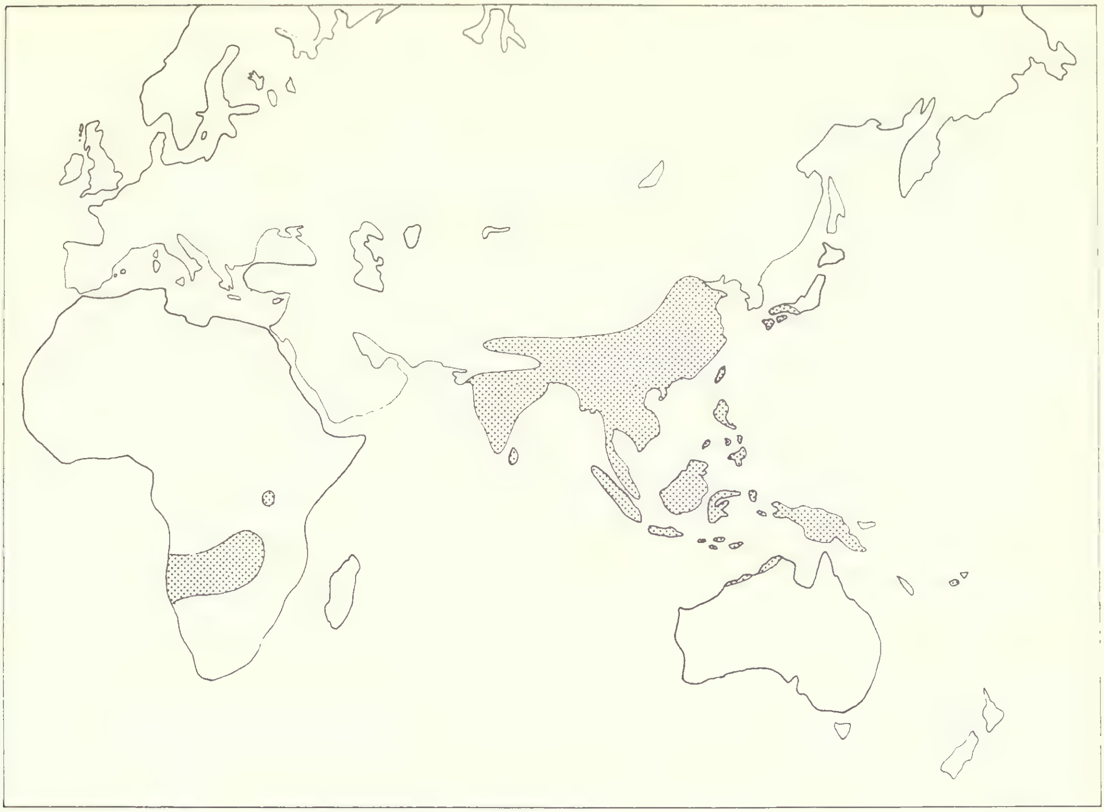

Fig. 31 Distribution of *Pogostemon sensu lato*.

7. Taxonomic conspectus

Key to genera and sections

1a. Anthers bilocular; disc with one or more tumescent lobes 2
1b. Anthers unilocular; disc without tumescent lobes 4

2a. Disc with four large, bright-red, tumescent lobes; upper tooth of calyx broad and overlapping the lateral teeth .... VI. **Tetradenia** (p. 70)
2b. Disc with one tumescent lobe; upper tooth of calyx not overlapping the lateral teeth 3

3a. Calyx with a well-defined annulus of white hairs at the mouth of the tube; mature nutlets one .... V. **Keiskea** (p. 70)
3b. Calyx without an annulus; mature nutlets usually four .... IV. **Elsholtzia** (p. 69)
ia. Bracteoles present; bracts longer than broad .... IVb. section **Aphanochilus** (p. 69)
ib. Bracteoles absent; bracts at least as broad as long ii
iia. Fruiting calyx inflated, much broader than at anthesis; nutlets verrucose; style tips clavate .... IVc. section **Platyelasma** (p. 70)
iib. Fruiting calyx sometimes enlarged but never inflated, not much broader than at anthesis; nutlets not verrucose; style tips subulate .... IVa. section **Elsholtzia** (p. 69)

4a. Bracts at least as broad as long, membranous, caducous; the whole plant covered in a dense indumentum of branched, stalked hairs 5
4b. Bracts longer than broad, not membranous, persistent; the indumentum variable but never of dense, branched, stalked hairs 7

5a. Mature nutlets with a pronounced rostrate tip; corolla with an entire upper lip, hairy disc-like excrescences at the base of the stamen filaments and a hairy crescent-shaped invagination at the base of the lower lip .... III. **Rostrinucula** (p. 68)
5b. Mature nutlets without rostrate tips; corolla with an emarginate upper lip and lacking excrescences at the bases of the stamen filaments and an invagination at the base of the lower lip 6

6a. Stamen filaments shortly hairy towards the base; corolla without an annulus of hairs .... II. **Leucosceptrum** (p. 68)
6b. Stamen filament completely glabrous; corolla with an annulus of hairs .... I. **Comanthosphace** (p. 68)

7a. Stamen filaments glabrous; upper lip of corolla emarginate 8
7b. Stamen filaments with long, often purplish hairs; upper lip of corolla entire .... VIII. **Pogostemon** (p. 71)
    iiia. All leaves opposite, usually petiolate; upper lip of corolla equalling or longer than the lower lip .... VIIIa. section **Pogostemon** (p. 71)
    iiib. At least some leaves in whorls of three or more, usually sessile; upper lip of corolla equalling or shorter than the lower lip .... VIIIb. section **Eusteralis** (p. 73)

8a. Calyx teeth plumose in fruit; corolla tube straight .... IX. **Colebrookea** (p. 74)
8b. Calyx teeth not plumose on fruit; corolla tube gibbous towards the base .... VII. **Eurysolen** (p. 70)

Conspectus

In the following conspectus diagnoses are given for supra-specific taxa only. Species are listed alphabetically within each genus and section. This study is concerned primarily with supra-specific groups and does not extend to an assessment of individual species. However, some species share very high similarity values and may well prove to be conspecific. In the conspectus species which are indented are possibly conspecific with the species which immediately precedes them.

I. **Comanthosphace** S. Moore in *J. Bot., Lond.* **15**:293 (1877).

Leaves ovate, petiolate; indumentum composed of branched and unbranched eglandular hairs; bracts at least as broad as long, membranous, caducous; bracteoles narrow, caducous; calyx sub-equally five-toothed; corolla bilabiate, upper lip emarginate, the throat with a complete (interrupted in *C. nanchuanensis*) annulus of hairs; stamen filaments glabrous, anthers unilocular; disc equal; mature nutlets four, sparsely hairy (glabrous in *C. nanchuanensis*). Pollen grains bi-nucleate/tri-colpate.

C. barbinervis (Miq.) S. Moore
C. formosana Ohwi
C. nanchuanensis C. Y. Wu & Li
C. ningpoensis (Hemsley) Hand.-Mazz.
C. stellipila (Miq.) S. Moore
    C. japonica (Miq.) S. Moore
    C. sublanceolata (Miq.) S. Moore

II. **Leucosceptrum** Smith, *Exot. bot.* **2**:113, t.116 (1805).

Leaves ovate, petiolate; indumentum composed of branched and unbranched eglandular hairs; bracts at least as broad as long, membranous, caducous; bracteoles narrow, caducous; calyx equally five-toothed; corolla bilabiate, upper lip very short, emarginate; stamen filaments shortly hairy towards the base, anthers unilocular; disc equal; mature nutlets four, glabrous. Pollen grains bi-nucleate/tri-colpate.

L. canum Smith

III. **Rostrinucula** Kudo in *Mem. Fac. Sci. Agric. Taihoku imp. Univ.* **2**(2):304 (1929).

Leaves ovate, petiolate; indumentum composed of branched and unbranched eglandular hairs;

bracts at least as broad as long, membranous, caducous; bracteoles narrow, caducous; calyx sub-equally five-toothed; corolla bilabiate, upper lip entire, the throat with an interrupted annulus of hairs borne on disc-like excrescences at the base of the stamen filaments and on a crescent-shaped invagination at the base of the lower lip; stamen filaments naked, anthers unilocular; disc equal; mature nutlets four, sparsely hairy, the apices extended to form a strongly-hooked beak. Pollen grains bi-nucleate/tri-colpate.
R. dependens (Rehder in Sargent) Kudo
R. sinensis (Hemsley) C. Y. Wu

IV. **Elsholtzia** Willd. in *Bot. Mag.* **4**:3 (1790).
Leaves narrowly ovate to orbicular, petiolate; indumentum composed of unbranched eglandular hairs or a mixture of unbranched glandular and eglandular hairs, sometimes with branched stalked hairs; verticils sometimes secund with one-many flowers; bracts linear to broader than long, sometimes membranous, persistent; bracteoles, when present, narrower than the bracts, persistent; calyx with five equal teeth or the upper three shorter than the lower two; corolla bilabiate, upper lip emarginate, the throat with or without an interruted annulus of hairs; stamen filaments glabrous, anthers bilocular, the locules confluent through partial fusion at the apex or free (*E. hunanensis*); disc with a single tumescent lobe; mature nutlets usually four, rarely one, glabrous. Pollen grains tri-nucleate/hexa-colpate.

IVa. Section **Elsholtzia**
    Cyclostegia Benth. in *Bot. Reg.* **15**: sub t. 1282 (1829).
    Elsholtzia section *Cyclostegia* (Benth.)Benth., *Lab. gen. sp.*:163 (1833).
Spikes usually secund, sometimes cylindrical; bracts at least as broad as long, usually membranous, veined, imbricate, the members of a pair sometimes fused to form a cyathium; bracteoles absent; fruiting calyx sometimes accresant but never inflated; style lobes subulate; nutlets rugulose or nearly smooth.
E. bodinieri Vaniot
E. ciliata (Thunb.) Hylander
E. concinna Vaut.
E. feddei Léveillé
    '*E. elegans* Franch.'—an apparently unpublished name applied by Merrill to material in E.
E. heterophylla Diels
E. hunanensis Hand.-Mazz.
E. kachinensis Prain
E. luteola Diels
E. oldhamii Hemsley
    E. argyi Léveillé
    E. nipponica Ohwi
    E. pseudocristata Léveillé & Vaniot
    E. soulei Léveillé
E. pygmaea W. Smith
E. strobilifera (Benth. in Wallich) Benth.

IVb. Section **Aphanochilus** (Benth.) Benth., *Lab. gen. sp.*:161 (1833).
    Aphanochilus Benth. in *Bot. Reg.* **15**: sub t. 1282 (1829).
Spikes usually cylindrical, rarely secund; bracts linear to ovate, not membranous or imbricate, always free; bracteoles similar to bracts but usually narrower; fruiting calyx sometimes accresant but never inflated; style lobes subulate; nutlets rugulose.
E. alopecuroides Léveillé & Vaniot
E. beddomei C. B. Clarke ex Hook. f.
E. blanda (Benth.) Benth.
E. capituligera (Dunn) C. Y. Wu
E. communis (Collett & Hemsley) Diels
E. elata Zoll. & Mor.
E. flava (Benth. in Wallich) Benth.

E. fruticosa (D. Don) Rehder
    Leucosceptrum plectranthoideum (Léveillé) Marquand
'*E. glanduligera*'—an unpublished name applied by C. B. Clarke to material in K which might represent a new species. More material is required for assessment.
E. griffithii Hook. f.
E. myosurus Dunn
E. ochroleuca Dunn
E. penduliflora W. Smith
E. pilosa (Benth. in Wallich) Benth.
    Dysophylla mairei Léveillé
E. pubescens Benth.
E. rugulosa Hemsley
E. stachyodea (Link) Raiz. & Saxena
E. stauntonii Benth.
E. winitiana Craib.

IVc. Section **Platyelasma** (Briq.) Press, **stat. nov.**
    Elsholtzia section *Aphanochilus* series *Platyelasmeae* Briq. in Engl. & Prantl, *Natürl. Pflanzenfam.* **4** (3a):327 (1897).
    Platyelasma Kitagawa in *Rep. Scient. Exped. Manchoukuo 1933*, **4** (2):26 (1935).

Spikes cylindrical; bracts at least as long as broad, not membranous or imbricate, free; bracteoles absent; fruiting calyx inflated in fruit; style lobes with clavate tips; nutlets verrucose.
E. densa Benth.
    E. manshurica (Kitagawa) Kitagawa
E. eriostachya (Benth. in Wallich) Benth.

V. **Keiskea** Miq. in *Annls Mus. bot. Lug.-Bat.* **2**:105 (1865).

Leaves ovate, petiolate; indumentum composed of unbranched eglandular hairs only; verticils secund, with two flowers; bracts ovate, not membranous, persistent; bracteoles absent; calyx five-toothed, the upper three teeth shorter than the lower two, the throat with an annulus of white hairs; corolla bilabiate, upper lip emarginate, the throat with a complete annulus of hairs; stamen filaments glabrous, anthers bilocular, the locules free; disc with a single tumescent lobe; mature nutlets one (?), glabrous and with a somewhat reticulate pattern of ridges. Pollen grains tri-nucleate/hexa-colpate.
K. elsholtzioides Merrill
K. glandulosa C. Y. Wu
K. japonica Miq.
K. sinenensis Diels
K. szechuanensis C. Y. Wu

VI. **Tetradenia** Benth. in *Bot. Reg.* **15**:sub t. 1300 (1829).

Leaves ovate, petiolate; indumentum composed entirely of unbranched eglandular hairs or mixed with branched stalked hairs; bracts broader than long, somewhat membranous, persistent; bracteoles absent; calyx five-toothed, the upper tooth much broader than, and overlapping, the two lateral teeth; corolla subilabiate, upper lip deeply emarginate, the throat with a complete annulus of hairs; stamen filaments glabrous, anthers bilocular, the locules confluent through partial fusion at the apex; disc with four bright-red, tumescent lobes equally spaced around the edge; mature nutlets four, glabrous. Pollen grains tri-nucleate/hexa-colpate.
T. fruticosa Benth.
    T. hildebrandtii Briq.
T. goudotii Briq.

VII. **Eurysolen** Prain in *Scient. Mem. med. Offrs Army India* **11**:43 (1898).

Leaves ovate, petiolate; indumentum composed of unbranched eglandular hairs only; bracts ovate, persistent; bracteoles similar but narrower, persistent; calyx subequally five-toothed; corolla bilabiate, upper lip emarginate, tube gibbous, the throat with an interrupted annulus of

hairs borne on disc-like excrescences at the base of the stamen filaments and on a papilla-like invagination on the ventral surface of the tube just below the gibbous curve; stamen filaments glabrous, anthers unilocular; disc equal; mature nutlets four, glabrous. Pollen grains bi-nucleate/tri-colpate.
E. gracilis Prain

VIII. **Pogostemon** Desf. in *Mem. Mus. Hist. nat. Paris* **2**:154 (1815).
Leaves linear to orbicular, sessile or petiolate; indumentum composed of unbranched eglandular hairs, unbranched eglandular and glandular hairs or branched sessile hairs; verticils sometimes subsecund; bracts linear to ovate, not membranous, persistent; bracteoles similar but narrower, persistent; calyx sub-equally five-toothed or with the three upper teeth shorter than the two lower; corolla bilabiate or subilabiate, upper lip entire; stamen filaments hairy in the middle or towards the base, the hairs long and often purplish, anthers unilocular; disc equal; mature nutlets four, rarely one, glabrous. Pollen grains bi-nucleate/tri-colpate.

VIIIa. Section **Pogostemon**
Dysophylla section *Oppositifoliae* Benth., *Lab. gen. sp.*:157 (1833).
Leaves in opposite pairs, usually petiolate; corolla with the upper lip equalling or longer than the lower lip.
P. amarantoides Benth. in DC.
P. andersonii (Prain) Press, **comb. nov.**
    Dysophylla andersoni Prain in *J. Asiat. Soc. Beng.* **59**:298 (1891).
P. atropurpureus Benth. in DC.
P. auricularius (L.) Hassk.
P. benghalensis (Burm. f.) Kuntze
    P. parviflorus (Benth. in Wallich) Benth.
P. brachystachyus Benth. in DC.
P. brevicorollus Y. Z. Sun
P. cablin (Blanco) Benth. in DC.
P. championii Prain
P. dielsianus Dunn
P. elsholtzioides Benth. in DC.
P. fraternus Miq.
P. formosanus Oliver in Hook.f.
P. gardneri Hook.f.
P. glaber Benth. in Wallich
P. glabratus Chermsirivathana ex Press, **sp. nov.**

(Fig. 32) A *P. auricularius* (L.) Hassk. caulibus et foliis glabris, nodis subito contractis, differt.
Herbae glabrae vel interdum remotis pilis eglandulatis. Caules subquadrangulati sulcis non profundis, nodis subito contractis. Folia opposita, 4–6 × 2–3 cm, ovata acuta cuneata, serrata vel dentata, petioli 2–5 mm. Inflorescentia terminalis ad 13 cm longa, densa, verticillastris numerosis multifloribus. Bracteae 2–3 mm longae, ovatae; bracteolae ad 2 mm longae, lanceolatae. Calyx campanulatus, tubo 1 mm longo, dentibus quinque 0·5 mm longis, triangularibus, sub fructu incurvatis. Corolla ± bilabiata purpurea, tubo 1·5 mm longo exserto, labio superiori 0·5 mm longo integro, lobis lateralibus labio superiori similibus, labio inferiori 0·5 mm longo integro. Stamina quator filamentis exsertis, pari inferiori longiori, prope medianum pilis longis barbatis; antherae uniloculares. Discus non lobatus. Nuculae maturae quatuor.
TYPE: Siam, Hin Dat, Kanburi, 14 July 1926, *Put* 132 (BM !-holotype). Other material: Siam, Ta Kanun, Kanburi, 'flowers pale purple, cultivated by Karens', 20 January 1926, *Kerr* 10274 (BM !)
LOCAL NAMES: Niam [Kerr]; Pak hom hang nu [Put].
Known only from the Kanburi area of Thailand.

P. griffithii Prain
P. heyneanus Benth. in Wallich
P. hirsutus Benth.
P. hispidus Prain
P. litigiosus Doan in Humbert

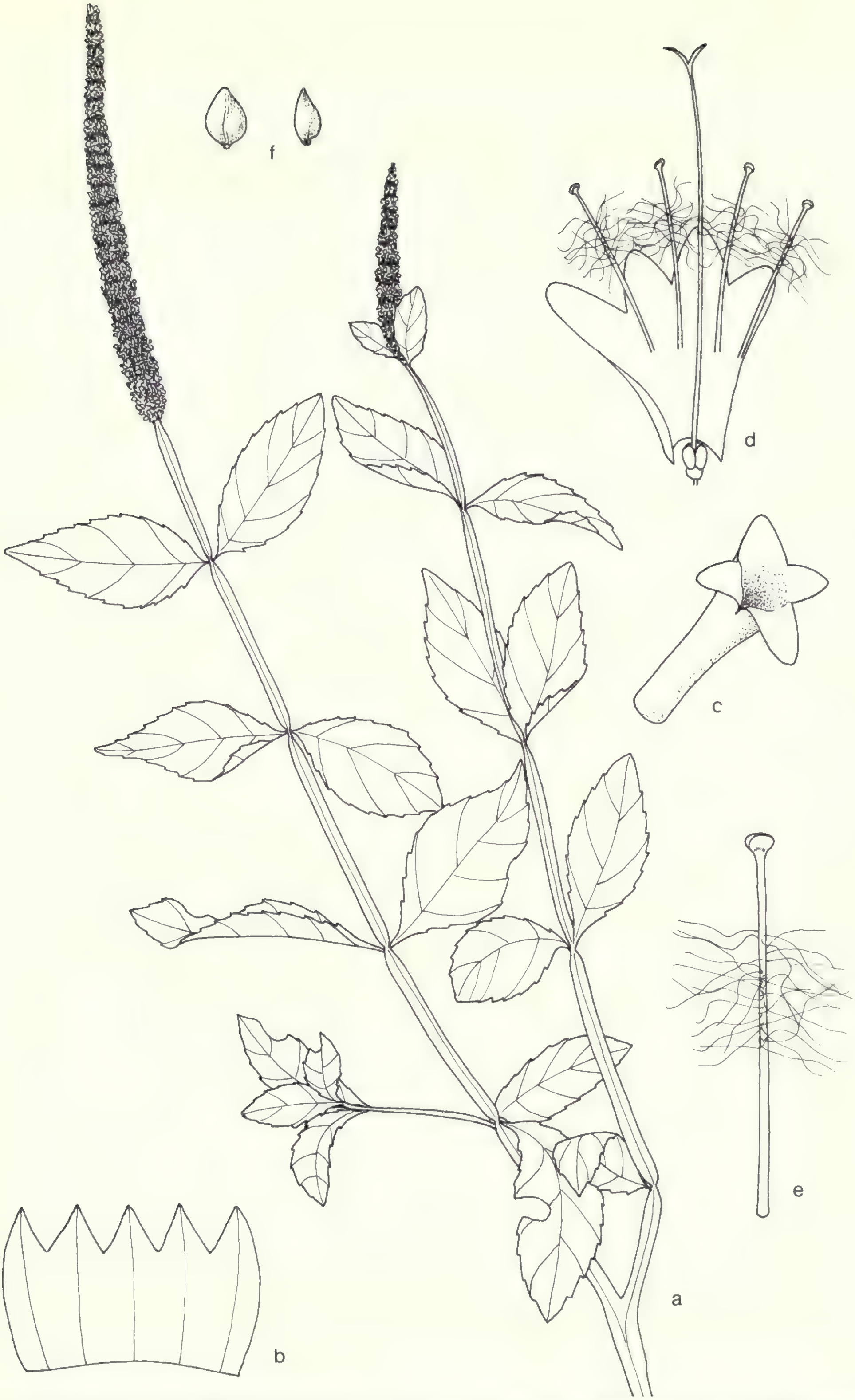

Fig. 32 *Pogostemon glabratus* Chermsirivathana ex Press [= '*Dysophylla glabrata*', see p. 19]. (a) habit × 1. (b) calyx × 20. (c) corolla × 20. (d) dissected flower × 20. (e) stamen × 40. (f) nutlet, inner face, and profile × 20.

P. macgregorii W. Smith
P. menthoides Blume
P. micangensis G. Taylor
P. mollis Benth.
P. mutamba (Hiern) G. Taylor
P. nelsonii Doan
P. nigrescens Dunn
P. nilagiricus Gamble
P. paludosus Benth. in DC.
P. paniculatus (Willd.) Benth. in Wallich
P. phillipensis S. Moore
P. pubescens Benth. in DC.
P. purpurascens Dalz. in Hook f.
P. reflexus Benth. in DC.
P. reticulatus Merrill
P. rotundatus Benth. in Wallich
P. myosuroides (Benth. in Wallich) Kuntze
    P. rugosus (Hook.f.) El-Gazzar & Watson
P. rupestris Benth.
P. salicifolius (Dalz. ex Hook.f.) Kuntze
P. speciosus Benth. in Wallich
P. strigosus Benth. in DC.
P. travancoricus Beddome
P. tuberculosus Benth. in Wallich
P. velatus Benth. in DC.
    P. williamsii Elmer
P. villosus Benth.
P. wattii C. B. Clarke
    P. battakianus Ridley
P. wightii Benth.

VIIIb. Section **Eusteralis** (Rafin.) Keng in *Fl. Males.* **8**(1):352 (1978).
    Eusteralis Rafin., *Fl. Tellur.* **2**(4):95 (1837).
    Dysophylla section *Verticillatae* Benth., *Lab. gen. sp.*:158 (1833).

At least some leaves in whorls of three or more, usually sessile; the corolla with the upper lip equalling or shorter than the lower lip.

P. aquaticus (C. H. Wright in Dyer) Press, **comb. nov.**
    Elsholtzia aquatica C. H. Wright in Dyer, *Fl. Trop. Afr.* **5**:451 (1900).
P. crassicaulis (Benth. in Wallich) Press, **comb. nov.**
    Dysophylla crassicaulis Benth. in Wallich, *Pl. As. Rar.* **1**:30 (1830).
P. cruciatus (Benth. in Wallich) Kuntze
P. deccanensis (Panigr.) Press, **comb. nov.**
    Eusteralis deccanensis Panigr. in *Phytologia* **32**(6):475 (1978).
    Dysophylla tomentosa Dalz. in *Hooker's J. Bot.* **2**:337 (1850), non *Pogostemon tomentosa* Hassk. (1844).
P. falcatus (C. Y. Wu) C. Y. Wu & Li
P. faurei (Léveillé) Press, **comb. nov.**
    Dysophylla faurei Léveillé in *Reprium Spec. nov. Regni veg.* **9**:248 (1911).
P. erectum Kuntze
    Dysophylla gracilis Dalz. in *Hooker's J. Bot.* **2**:337 (1850), non *Pogostemon gracilis* Hassk. (1843).
P. griffithii (Hook.f.) Press, **comb. nov.**
    Dysophylla griffithii Hook.f., *Fl. Brit. India* **4**:641 (1885).
P. helferi (Hook.f.) Press, **comb. nov.**
    Dysophylla helferi Hook.f., *Fl. Brit. India* **4**:640 (1885).

P. koehneanus (Muschler) Press, **comb. nov.**
    Dysophylla koehneana Muschler in *Reprium nov. Spec. Regni veg.* **4**:269 (1907).
P. linearis (Benth. in DC.) Kuntze
P. lythroides (Diels) Press, **comb. nov.**
    Dysophylla lythroides Diels in *Notizbl. bot. Gart. Mus. Berl.* **9**:1031 (1926).
P. peguanus (Prain) Press, **comb. nov.**
    Dysophylla peguana Prain in *J. Asiat. Soc. Beng.* **59**:298 (1891).
P. pentagonus (C. B. Clarke ex Hook.f.) Kuntze
P. pumilus (Graham) Press, **comb. nov.**
    Mentha pumila Graham in *Edinb. New phil. J.* **4**:393 (1828) [non Host (1831)].
    Dysophylla pumila (Graham) Benth. in Wallich, *Pl. As. Rar.* **1**:30 (1830).
P. quadrifolius (Benth. in Wallich) Kuntze
P. sampsonii (Hance) Press, **comb. nov.**
    Dysophylla sampsoni Hance in *Annls Sci. nat.* V, **5**:284 (1866).
P. stellatus (Lour.) Kuntze
P. stocksii (Hook.f.) Press, **comb. nov.**
    Dysophylla stocksii Hook.f., *Fl. Brit. India* **4**:642 (1885).
P. szemacensis (C. Y. Wu & Hsuan) Press, **comb. nov.**
    Dysophylla szemacensis C. Y. Wu & Hsuan in *Acta phytotax. sin.* **10**:238 (1967).
P. trinervis Chermsirivathana ex Press, **sp. nov.**

Fig. 33. Inter species section *Eusteralis* (Rafin.) Keng foliis latis triplinervibus distinguilibus.
Herbae hirtae parcae pilis glanduliferis vel eglandulatis. Caules ad 30 cm longi, bases versus prostratae supra erectae ad nodos radicantes. Folia sessilia in verticilli e tres dispositi, 6–13 × 4–7 mm, ovata vel rotundata, acuta vel obtusa, cuneata, serrata vel dentata, triplinervia nervo medio et pari laterali impresso subtus elevata. Inflorescentiae terminales, ad 5 cm longae, bases interruptes, verticillastris 5–10 (–15), flores 6–20 in omnis verticillaster. Bracteae 2–3 mm longae, lineares; bracteolae ad 2 mm longae, lineares vel lineares-subulatae. Calyx campanulatus, tubo 1–1·5 mm longo, dentibus quinque 0·5 mm longo, triangularibus sub fructu erectis vel leviter patentibus. Corolla ± bilabiata purpurea, tubo 0·75 mm longo exserto integro, lobis lateralibus labio superiori similibus, labio inferiori 0·25 mm longo integro. Stamina quatuor filamentiis exsertis, pari superiori longiori, prope medianum pilis longis barbatis; antherae uniloculares. Discus non lobatus. Nuculae maturae quatuor.
TYPE: Siam, Hui Taleng, Korat, 24 December 1928, *Put* 2223 (BM !-holotype). Other material: Siam, Korat, Pak Tong Chai, 'flowers purple; among short grass on open ground', c. 200 m, 25 December 1923, *Kerr* 8115 (BM).
Known only from the Korat area of Thailand.

P. tsiangii (Y. Z. Sun) Press, **comb. nov.**
    Dysophylla tsiangii Y. Z. Sun in *Acta phytotax. sin.* **11**:50 (1966).
P. yatabeanus (Makino) Press, **comb. nov.**
    Dysophylla yatabeanus Makino in *Bot. Mag., Tokyo* **1**:55 (1898).

IX. **Colebrookea** Smith, *Exot. bot.* **2**:111, t.115 (1805).
Leaves ovate, petiolate; indumentum composed of unbranched eglandular hairs only; bracts linear, not membranous, persistent; bracteoles similar but smaller, persistent; calyx with five equal, long, slender, plumose teeth; corolla bilabiate, upper lip emarginate; stamen filaments glabrous, anthers unilocular; disc equal; mature nutlets one, hairy. Pollen grains bi-nucleate/tri-colpate.
C. oppositifolia Smith
    C. ternifolia Roxb.

Species excludendae
Elsholtzia integrifolia Benth. = *Schizonepeta tenuifolia* (Benth.) Briq.
'Elsholtzia japonica' sensu d'Argy, *non* Miq. = *Agastache* sp. (? *rugosus* Fisch. & Mey.).

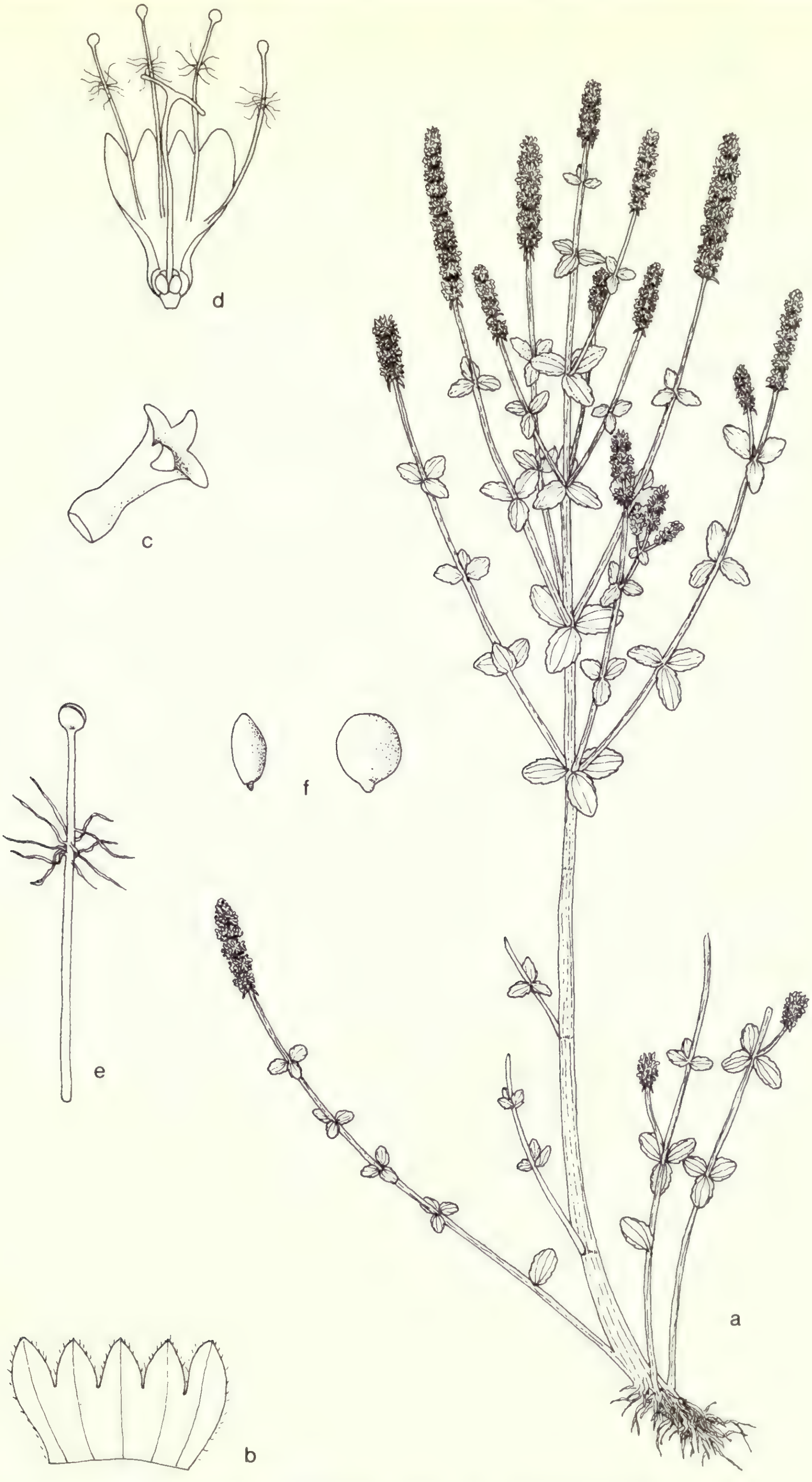

Fig. 33 *Pogostemon trinervis* Chermsirivathana ex Press [= '*Dysophylla trinervia*,' see p. 14]. (a) habit × 1. (b) calyx × 20. (c) corolla × 20. (d) dissected flower × 20. (e) stamen × 40. (f) nutlet, inner face, and profile × 20.

Appendix 1. Specimens used for scoring and producing averaged data

For the names to which the acronyms refer see Table 2.

EGRA 1: *Put* in Herb. Kerr 4404 (BM), *Robinson & Kloss* 130 (BM), s.n. 1914 (BM). EJAP 2: *d'Argy* s.n. Kiangsu (E). EFED 3: *Forrest* 22386 (E), *Soulie* 227 (E—holotype). EELE 4: *Bau Hwa Shan* 1490 (E). EPSE 5: *Taquet* 1223 (K—paratype), 1224 (K—paratype). ENIP 6: *Ikeo* 9567 (TI—isotype), *Kurata* s.n. 1964 (BM), *Mayebara* 4125 (TI). EOLD 7: *Oldham* s.n. 1864 (K—holotype), *Tagawa* 4162 (TI), *Yamazaki* 3059 (TI). ECON 8: *Ludlow & Sherriff* 9057 (BM), *Polunin* 1020 (BM), 1612 (BM). ECIL 9: *Togasi* 787 (BM), *Wilson* 5717 (BM), *Yu* 10728 (BM). EKAC 10: *Forrest* 6729 (E), *Kingdom-Ward* 20365 (BM), *Put* in Herb. Kerr 3478 (BM). EPYG 11: *Forrest* 17128 (E—holotype). ESOU 12: *Maire* 321 (E), 599 (E), *Soulie* 226 (E—holotype). EARG 13: *Cavalerie* 7993 (E), *Léveillé* s.n. (E). ELUT 14: *Forrest* 11145 (E), 15184 (E), *Yu* 13952 (BM). EBOD 15: *Bodinier* 2 (E—holotype), *Forrest* 2997 (BM), 7371 (BM). EHET 16: *Forrest* 934 (E—holotype), *Maire* 1203 (E), [Collector unknown] 096035 (TAI). ESTR 17: *Ludlow, Sherriff & Taylor* 7139 (BM), *Nicolson* 2652 (BM), *Stainton, Sykes & Williams* 8526 (BM). EHUN 18: *Handel-Mazzetti* 2702 (E—isotype). EERI 19: *Dhwoj* 0180 (BM), *Ludlow, Sherriff & Hicks* 16682 (BM), *Stainton, Sykes & Williams* 8102 (BM). EDEN 20: *Ludlow, Sherriff & Elliot* 14130 (BM), *Stainton, Sykes & Williams* 2169 (BM), 8102 (BM). EMAN 21: *Nakai, Honda & Kitamura* s.n. 1933 (TI—holotype), *Togashi* 828 (TI), 1578 (TI). EAQU 22: *Johnson* 15 (K—holotype), *Fanshawe* 8503 (K), 8512 (K). EINT 23: *Staunton* s.n. (BM—holotype). EBED 24: *Beddome* 147 (BM—holotype), *MacGregor* 69 (E), 608 (E). EPEN 25: *Forrest* 11686 (E—holotype), *Yu* 17600 (E). ERUG 26: *Forrest* 6527 (BM), *Maire* 633 (E), *Yu* 16748 (E). ESTA 27: *Jackson* s.n. 1929 (BM), *Licent* 2996 (BM), *Staunton* s.n. (BM—holotype). EFLA 28: *Forrest* 6283 (BM), *Stainton* 5090 (BM), *Wallich* 1553 (BM—isotype). EFRU 29: *McLaren's native collectors* 326d (BM), *Polunin, Sykes & Williams* 3126 (BM), *Young* s.n. 1880 (BM). EPUB 30: *Horsefield* 337 (BM). ECOM 31: *Maire* 561 (BM), *Yu* 14498 (BM), 14712 (BM). EALO 32: *Cavalerie* 1426 (E—holotype). EGRI 33: *Haines* s.n. 1914 (E), *Lace* 4391 (E). EGLA 34: *Clarke* 37393 (K). EELA 35: *Koorders* 37621B (K), Herb. Kuntze 5613 (K),*Ridley* s.n. 1915 (K). EWIN 36: *Kerr* 1607 (BM), s.n. (BM), *Put* in Herb. Kerr 4412 (BM). ESTC 37: *Buchanan* s.n. 1802 (BM—holotype of *Elsholtzia leptostachya*), *Clarke* 23765 (BM), *Polunin, Sykes & Williams* 5827 (BM). EBLA 38: *Ludlow, Sherriff & Taylor* 7075 (BM), *Norkett* 8631 (BM), *Stainton, Sykes & Williams* 8323 (BM). EMYO 39: *Forrest* 7220 (E—holotype), *Wilson* 3533a (K). EOCH 40: *Maire* s.n. (E—holotype of *Elsholtzia lampradena*). EPIL 41: *Forrest* 28965 (BM), *Maire* 1204 (BM), *Stainton, Sykes & Williams* 4452 (BM). ECAP 42: *Forrest* 1680 (BM), 20697 (BM), 22956 (BM). DTRI 43: *Kerr* 8115 (BM), *Put* in Herb. Kerr 2223 (BM). DHEL 44: *Helfer* 194 (BM), 3968 (K—holotype). DTOM 45: *Buchanan* s.n. (BM), *Hohenacker* 371 (BM), *Young* s.n. 1879 (BM). DPEN 46: *Carlke* 20438 (BM—isotype), *Garrett* in Herb. Kerr 59 (BM), *Kerr* 1465 (BM). DSTO 47: *Stocks* s.n. in Herb. Hooker (K—holotype). DSAM 48: *Sampson* in Herb. Hance 10946 (BM—holotype). DPEG 49: *Kurz* 2401 (K), 2405 (K), *Put* in Herb. Kerr 1971 (BM). DGRI 50: *Chattaya* 5224 (K), *Gamble* 13748 (K), *Griffith* 3968 (K). DYAT 51: *Science College imp. Univ. Japan* s.n. 1883 (K—isotype), *Tanaka* 7338 (TAI). DCRA 52: *Clarke* 23691 (BM), *Griffiths* 1024 (BM), *Wallich* 1545 (BM—isotype). DSTE 53: *Clarke* 8073 (BM), *Loureiro* s.n. (BM—holotype), *Simpson* 9189 (BM). DLIN 54: *Clarke* 45731 (BM), *Kingdom-Ward* 14260 (BM), *Ludlow, Sherriff & Hicks* 21019 (BM). DCRU 55: *Beddome* s.n. (BM), *Clarke* 18059 (BM), *Polunin, Sykes & Williams* 5875 (BM). DQUA 56: *Roxburgh* s.n. (BM—isotype), *Rugel* s.n. (BM), *Wallich* 1538 (BM). DTSI 57: *Tsiang* 9449 (KUN—isotype). DFAL 58: *Wang* 79441 (KUN—isotype). DSZE 59: *Tsiang* 12713 (KUN—isotype). DFAU 60: *Faurie* 760 (E—holotype). DKOE 61: *Hosseus* 704 (BM—isotype). DGRA 62: *Dalzell* s.n. (K—holotype), *Stocks & Law* s.n. Malabar & Concan (BM). DLYT 63: *Fan & Li* 563 (BM). DPUM 64: *Wallich* 1546 (K). DMAI 65: *Maire* s.n. 1911 (E—holotype). DAND 66: *Anderson* s.n. 1867 (K—holotype). DGLA 67: *Kerr* 10274 (BM), *Put* in Herb. Kerr 132 (BM). DAUR 68: *Clarke* 26464 (BM), *Forbes* 89 (BM), *Stainton, Sykes & Williams* 6481 (BM). DSAL 69: *Dalzell* s.n. (K—holotype), *Lain* s.n. in Herb. Hooker (K), *Young* s.n. 1882 (BM). DRUG 70: *Beddome* s.n. (BM), Herb. Rottler s.n. 1828 (K), *Wallich* 1547 (K-W—holotype). DMYO 71: *Fricker* 4724 (K), *Koenig* s.n. (BM), *Wallich* 1547 (K-W—holotype). PBEN 72: *Roxburgh* s.n. India (BM), *Stainton* 13 (BM), 5220 (BM). PPAR 73: *Andrews* 348 (BM), *Beddome* s.n. (BM), *Metz* 1393 (BM). PPAN 74: *Stocks & Law* s.n. Malabar & Concan (BM), *Thomson* s.n. Mont. Nilghiri & Kurg. (BM), *Wallich* 1561 (BM). PTUB 75: *Clarke* 26368 (BM), *Ludlow, Sherriff & Taylor* 6759 (BM), *Sarail* 23 (BM). PGLA 76: *Flatt* 161 (BM), *Hooker* s.n. Sikkim (BM), *Nicolson* 2941 (BM). PHEY 77: *MaCrae* 737 (BM), *Robinson & Kloss* 88 (BM), *Thomson* s.n. Maisor (BM). PCAB 78: *Clemens* s.n. 1924 (BM), *Horsefield* s.n. Java (BM), *Ramos* 22432 (BM). PELS 79: *Griffiths* 1018 (BM), *Kingdom-Ward* 14234 (BM), *Ludlow, Sherriff & Taylor* 7211 (BM). PAMA 80: *Hooker* s.n. Sikkim (BM), *Murata* 06306529 (BM), *Stainton, Sykes & Williams* 9276 (BM). PFOR 81: *Kao* 4883 (TAI), *Kudo & Mori* 2401 (TAI), *Simada* 5419B (TAI). PMEN 82: *J. & M. S. Clemens* 32575 (BM), 40267 (BM), *Pételot* 5110 (BM). PFRA 83: *Clarke* 44065 (BM), *Horsefield* s.n. Java (BM), *Kerr* 9658 (BM). PBRA 84: *Clarke* 40303 (BM), *Griffiths* 222 (BM), *Hooker & Thomson* s.n. Khasia (BM). PMIC 85: *Gossweiler* 2545 (BM—isotype), 9668 (BM), *Raynal* 12161 (BM). PMUT 86: *Gossweiler* 12134 (BM), *Welwitsch* 5496 (BM), 5990 (BM—holotype). PNIG 87: *Henry* 9082 (K), 11174 (K—holotype), 12563 (K). PPHI 88: *Ramos* 33320 (BM), *Ramos & Edano* 45012 (BM), *Whitehead* s.n. 1896 (BM—holotype). PREF 89: Herb. Hooker 80 (K), *Thwaites* 154 (BM), *Walker* s.n. Ceylon (K—lectotype). PRET 90: *Ahern's collector* Forestry Bureau no. 3395 (BM—holotype), *Edano* 48842 (BM). PMOL 91: *Clarke* 10673 (BM), *Gardner* s.n. in Herb. Miers (BM), *Vine* 216 (BM). PTRA 92: *Beddome* 109 (BM—holotype). PATR 93: *Beddome* s.n. Anamallays (BM), s.n. W. slopes of Nilgherries (BM), *Herb. Wight* 2127 (K—holotype). PSPE 94: *Metz* 1225 (BM), *Schmidt* s.n. Nilghiries (BM), *Vine* 215 (BM). PVEL 95: *Cuming* 1097 (BM—isotype), *MaGregor* 11339 (BM), *Mendoza* 40923 (BM). PWIL 96: *Elmer* 22225 (BM—isotype). PPUR 97: Herb. Dalzell s.n. (K—holotype), *Stocks* s.n. Concan (BM), *Vasnoli* s.n. 1881 (BM). PPAL 98: *Gamble* 17853 (BM). PVIL 99: *Masters* s.n. in Herb. Hooker (K), *Roxburgh* s.n. India (BM), *Wallich* s.n. 1831 (K). PWIG 100: *Gamble* 18389 (BM), *Schmidt* 74 (BM), *Stocks & Law* s.n. Malabar, Concan (BM). PROT 101: *Lawson* s.n. 1884 (BM), *Wallich* 1535 (K-W—holotype). PSTR 102: *Clarke* 5501 (BM), 15617 (BM), *Kingdom-Ward* 18763 (BM). PHIS 103: Herb. Hooker s.n. (K), *Jenkins* 346 in Herb. Hooker (K—paratype), *Kerr* 6631 (BM). PPUB 104: *Kerr* 2384 (BM), 3113 (BM), *Pételot* 5297 (BM). PBRE 105: *Chen* 3206 (KUN—isotype). PNEL 106: Cook's 3rd voyage s.n. (BM). PBAT 107: *Ridley* s.n. 1921 (K—holotype). PWAT 108: *Clarke* 41719 (K—holotype). PHIR 109: *Beddome* s.n. (BM), *Simpson* 9049 (BM), *Thwaites* 283 (BM). PRUP 110: *Cramer* 4277 (K), *MaCrae* 396 (K—holotype), *Thwaites* 343 (BM). PMAC 111: *Hansen & Smitinand* 12661 (K), *Iwatsuki, Fukuoka & Chintayungkun* 9659 (K). PGAR 112: *Gardner* 1847 (K—holotype), Herb. Wight s.n. (K), *V. Row* 3229 (K). PCHA 113: *Champion* 339 (K—holotype), *Shiu Ying Hu* 12421 (K). PDIE 114: *Forrest* 875 (K—isotype). PGRI 115: *Griffith* 3962 (K—holotype). PNIL 116: *Bourne* 5094 (K), Herb. Hooker s.n. (K). PLIT 117: *Evrard* 1834 (K), *Poilane* 24241 (K), s.n. (K). RDEP 118: *Cavalerie* s.n. in Herb. Léveillé (E), *Wilson* 3534 (E—holotype), 4313 (BM). RSIN 119: *Bodinier* 2709 (E—holotype of *Leucosceptrum bodinieri*), *Henry* 7765 (E—holotype). CFOR 120: *Huang* 7040 (TAI), *Huang & Hsieh* 7297 (TAI), *Kao* 8611 (TAI). CSTE 121: *Murata* 19058 (TI), 19171 (TI), 36037 (TI). CBAR 122: *Humsawa* s.n. 1947 (TI), *Kanai* 6012 (TI), *Yamozaki* 6 (TI). CSUB 123: *Bisset* 102285 (BM), *Hara* s.n. 1953 (TI), *Togasi & Matsuoka* 180 (BM). CJAP 124: *Maximovicz* s.n. 1862 (BM), in Herb. Hance 13214 (BM), *Tschonoski* s.n. 1864 (BM). CNIN 125: *Law* 1012 (TAI), *Liou* 1378 (E), *Handel-Mazzetti* 2602 (E). LCAN 127: *Bowes Lyon* 37 (BM), *Ludlow, Sherriff & Taylor* 6475 (BM), *Stainton* 5140 (BM). LPLE 128: *Maire* s.n. (E—holotype). TGOU 129: *Goudot* s.n. (G), *Hildebrandt* 3471 (G—holotype). THIL 130: *Hildebrandt* 3971 (G—holotype). TFRU 131: *Forsythe-Major* s.n. 1895 (G), *Lyle* 278 (K—holotype). KJAP 132: Bot. gard. Tokyo s.n. 1880 (TI), Herb. Terasaki s.n. 1906 (K),*Yano* s.n. 1890 (TI). KELS 133: *Jiangsu group* 2667 (KUN). KGLA 134: *Y. Ling* 728 (KUN—isotype). KSIN 135: *Chen Quan* 999 (KUN). KSZE 136: *T. P. Tsung* 39354 (KUN—isotype). CTER 137: *Roxburgh* s.n. Mysore (BM), s.n. Mysore Bot. gard. Calc. (BM—isotype?), s.n. Hort. Calc. (BM). COPP 138: *Clarke* 3464B (BM), *Hooker* s.n. Sikkim (BM), *Thomson* s.n. Mont. Nilghiri & Kurg. (BM).

Appendix 2. Coded data for 139 OTUs

EGRA1	0	15	0	*	0	1	1	0	1	0	1	0	0	1	20	1	75	50	0	10	300	350	0	1	1	1	0	0	1	400	0	100	100	1	0	0	0	1	1	0	0	2	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	2	25	0	30	30
EJAP2	0	20	0	*	0	1	2	1	1	0	0	0	0	1	20	1	200	100	0	15	300	300	0	1	1	1	0	0	1	300	0	150	250	*	*	*	0	0	0	0	0	0	2	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	1	12	0	16	10
EFED3	0	10	0	*	0	1	0	2	1	1	2	0	0	0	*	1	200	100	0	10	100	400	0	1	1	1	0	0	1	400	0	100	150	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	15	2	6	10
EELE4	0	10	0	*	0	1	0	1	1	1	2	0	0	0	*	1	150	100	0	10	150	400	0	1	1	1	0	0	1	500	0	150	200	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	15	2	8	10
EPSE5	0	10	0	*	0	1	1	0	1	1	2	0	0	0	*	1	150	100	0	5	100	*	0	*	1	1	0	0	1	300	0	100	150	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	15	2	10	5
ENIP6	0	15	0	*	0	1	1	0	1	1	2	0	0	0	*	1	50	50	0	10	100	250	0	1	1	1	0	0	1	300	0	100	100	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	15	2	6	10
EOLD7	0	40	0	*	0	1	1	0	1	1	2	0	0	0	*	1	100	100	0	10	100	*	0	1	1	1	0	0	1	400	0	100	100	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	20	2	6	10
ECON8	0	15	0	*	0	1	0	0	1	0	2	0	0	0	*	1	300	200	0	10	150	200	0	1	1	1	0	0	1	300	0	100	100	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	2	2	1	12	0	8	10
ECIL9	0	30	0	*	0	1	1	0	2	1	2	0	0	0	*	1	100	200	0	5	150	200	0	1	1	1	0	0	1	300	0	50	50	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	20	2	10	10
EKAC10	0	5	0	*	0	2	2	2	1	0	2	0	0	0	*	0	25	25	0	10	100	150	0	1	0	0	0	0	1	400	0	100	150	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	15	0	10	3
EPYG11	0	3	0	*	0	0	1	0	1	1	2	0	0	0	*	1	100	75	0	5	200	*	0	1	1	1	0	0	1	600	0	100	100	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	*	1	0	0	0	1	1	1	15	2	1	5
ESOU12	0	15	0	*	0	1	1	2	1	1	2	0	0	0	*	1	150	75	0	10	100	300	0	1	1	1	0	0	1	300	0	100	150	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	15	2	10	10
EARG13	0	20	0	*	0	1	1	0	1	1	2	0	0	0	*	1	100	100	0	10	100	200	0	1	1	1	0	0	1	250	0	50	50	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	2	1	2	20	2	4	5
ELUT14	0	2	0	*	0	1	1	1	1	1	2	1	0	0	*	1	100	50	0	5	100	100	0	1	1	1	0	0	1	400	0	100	100	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0	1	20	2	6	10
EBOD15	1	1	0	*	0	1	0	0	1	1	2	1	0	0	*	0	150	150	0	10	150	*	*	*	1	0	0	0	1	950	0	150	200	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	*	*	*	*	1	0	0	0	0	0	0	15	0	10	10
EHET16	1	1	0	*	0	1	0	0	1	1	2	1	0	0	*	0	50	50	0	10	150	500	0	1	1	0	0	0	1	800	0	100	100	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	20	0	10	10
ESTR17	0	1	0	*	0	1	0	0	1	1	2	1	0	0	*	1	100	50	0	5	150	200	0	1	1	1	0	0	1	500	0	50	50	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	30	0	6	5
EHUN18	0	45	0	*	0	1	0	0	1	1	2	0	0	0	*	1	100	50	0	5	100	*	0	*	1	1	0	0	1	200	0	100	100	0	0	1	2	0	0	0	0	0	2	0	0	0	0	1	1	*	*	*	*	1	0	0	0	1	1	1	20	0	2	10
EERI19	0	5	0	*	0	1	0	1	1	0	2	0	0	0	*	1	100	100	0	10	100	250	0	1	1	1	0	0	1	100	1	50	75	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1	0	1	0	1	1	2	15	0	20	10
EDEN20	0	10	0	*	0	1	0	1	1	0	2	0	0	0	*	1	50	50	0	10	100	500	0	1	1	1	0	0	1	150	1	25	50	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0	1	1	0	0	0	1	1	1	7	0	16	10
EMAN21	0	10	0	*	0	1	1	1	1	0	2	0	0	0	*	0	50	50	0	5	50	400	0	1	1	1	0	0	1	150	0	50	50	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	1	1	1	15	0	8	5
EAQU22	0	0	1	5	0	0	1	1	1	0	0	0	0	1	30	0	50	50	0	5	100	200	0	0	1	1	0	0	1	150	1	100	150	0	0	1	0	0	0	1	0	1	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	15	0	40	10
EINT23	0	3	0	*	0	3	1	1	0	0	0	0	0	1	20	0	75	75	0	15	150	250	0	0	1	1	0	1	1	200	0	50	100	*	*	*	0	0	0	0	0	2	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	12	0	12	10
EBED24	0	10	0	*	0	1	0	2	1	0	1	0	0	2	15	0	50	50	0	10	100	150	0	1	1	1	0	0	1	250	0	100	150	*	*	*	2	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	2	2	30	0	20	5
EPEN25	0	5	0	*	0	1	0	1	2	0	0	0	0	1	10	0	100	100	0	10	200	400	0	1	0	0	0	0	0	200	0	100	100	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	1	1	25	0	10	30
ERUG26	0	15	0	*	0	1	0	1	1	0	0	0	0	1	20	0	100	100	0	10	100	200	0	1	1	1	0	0	1	300	0	200	200	0	1	0	2	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	2	2	20	0	40	30
ESTA27	0	20	0	*	0	1	1	1	1	0	0	0	0	1	20	0	100	100	0	5	120	400	0	1	1	1	0	0	1	400	0	100	100	0	0	2	2	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	1	1	25	0	20	30
EFLA28	0	80	0	*	0	1	1	1	1	0	1	0	0	2	10	0	100	100	0	10	200	500	0	1	1	1	0	0	1	500	0	100	100	0	1	0	2	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0	2	15	0	18	20

EFRU29	0	40	0	*	0	1	1	0	2	0	0	0	0	2	20	0	50	50	0	10	150	300	0	1	1	1	0	0	1	300	0	100	100	1	1	0	2	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	1	0	1	0	2	1	2	40	0	24	10
EPUB30	0	10	0	*	0	1	1	1	1	0	0	0	0	1	20	1	75	50	0	10	50	*	0	*	1	1	0	0	1	200	0	50	100	0	1	0	2	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	*	1	0	0	0	2	1	2	20	0	35	5
ECOM31	0	5	0	*	0	1	1	0	1	0	0	0	0	1	20	1	200	100	0	10	100	400	0	1	1	1	0	0	1	300	0	100	150	0	0	1	2	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	20	0	30	5
EALO32	0	10	0	*	0	1	1	0	1	0	0	0	0	1	30	1	100	75	0	10	150	350	0	1	1	1	0	0	1	300	0	100	100	0	0	1	2	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	2	2	2	30	0	20	10
EGRI33	0	2	0	*	0	1	1	1	1	0	0	0	0	1	25	1	100	75	0	10	125	*	*	*	1	1	0	0	1	250	0	100	100	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	*	*	*	*	1	0	0	0	2	2	1	20	0	24	0
EGLA34	0	1	0	*	0	1	0	0	1	0	0	0	0	1	20	1	100	50	0	10	*	150	0	1	1	1	0	0	1	*	*	100	100	*	*	*	2	0	0	1	0	*	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	2	20	0	12	10
EELA35	0	5	0	*	0	1	0	1	1	0	0	0	0	1	30	1	100	50	0	10	125	300	0	1	1	1	0	0	1	200	0	50	100	*	*	*	2	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	2	2	15	0	20	10
EWIN36	0	10	0	*	0	1	1	1	1	0	0	0	0	1	20	0	25	25	0	10	100	250	0	1	1	1	0	0	1	125	0	25	40	1	0	0	2	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	2	2	2	40	0	24	5
ESTC37	0	30	0	*	0	1	1	1	1	0	0	0	0	1	20	1	150	100	0	10	100	200	0	1	1	1	0	0	1	200	0	50	75	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	1	1	1	0	1	1	1	40	0	16	5
EBLA38	0	5	0	*	0	1	1	1	1	0	0	0	0	1	10	1	50	40	0	10	100	200	0	1	1	1	0	0	1	200	0	75	100	1	0	0	2	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	1	40	0	24	10
EMYO39	0	5	0	*	0	1	1	1	1	0	0	0	0	1	20	1	100	75	0	10	100	*	0	*	1	1	0	0	1	200	0	50	100	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	1	*	*	*	*	1	0	1	0	2	2	2	60	0	20	10
EOCH40	0	10	0	*	0	1	1	2	1	0	0	0	0	2	10	1	100	50	0	10	100	*	0	1	1	1	0	0	1	300	0	75	50	1	0	0	2	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	*	1	0	1	0	1	1	1	20	0	12	10
EPIL41	0	10	0	*	0	1	1	1	1	0	0	0	0	1	70	1	300	200	0	10	100	200	0	1	1	1	0	0	1	300	0	100	150	0	0	1	2	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	1	20	0	12	10
ECAP42	0	1	0	*	0	1	0	0	1	0	0	0	0	1	30	0	150	150	0	10	200	300	0	1	1	1	0	0	1	400	0	150	150	0	1	0	2	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	1	0	1	0	2	2	2	4	0	10	0
DTRI43	0	0	1	3	0	2	0	2	1	0	0	0	0	1	20	0	50	50	0	5	50	100	0	1	1	1	0	0	0	75	0	25	25	0	0	1	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	10	0	12	5
DHEL44	0	0	1	5	0	0	3	0	1	0	1	0	0	2	15	0	50	50	0	*	100	150	0	1	1	1	0	0	0	100	0	50	50	*	*	*	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	12	0	6	0
DTOM45	0	0	1	6	0	0	3	0	0	0	0	0	0	1	20	0	50	50	0	*	50	125	0	1	1	1	0	0	0	100	0	50	50	0	0	1	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	30	0	9	0
DPEN46	0	0	1	4	0	0	3	1	0	0	0	0	0	1	20	0	50	50	0	5	50	100	0	0	1	1	1	0	0	100	0	100	150	*	*	*	0	0	0	0	0	*	0	2	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	20	0	12	0
DSTO47	0	0	1	14	0	0	3	0	0	0	0	0	0	1	10	0	50	50	0	5	50	100	0	0	1	1	1	0	0	100	0	50	75	*	*	*	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	50	0	*	0
DSAM48	0	0	1	3	0	0	0	1	1	0	0	1	0	1	15	0	100	100	0	5	150	150	0	1	1	1	0	0	0	200	0	50	75	0	0	1	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	20	0	15	0
DPEG49	0	0	1	4	0	0	3	1	0	0	0	0	0	1	20	0	75	75	0	5	100	150	0	1	1	1	0	0	0	125	0	50	75	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	20	0	15	0
DGRI50	0	0	1	4	0	0	3	1	0	0	0	0	0	1	20	0	50	50	0	5	50	150	0	0	1	0	1	0	0	150	0	50	50	*	*	*	0	0	0	0	0	*	0	2	0	*	0	0	0	0	0	0	1	1	0	0	0	0	0	0	40	0	*	*
DYAT51	0	0	1	4	0	0	3	1	1	0	0	0	0	1	25	0	100	100	0	*	100	200	0	1	1	1	0	0	0	150	0	100	100	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	15	5	*	0
DCRA52	0	0	1	4	0	0	3	1	1	0	0	0	0	1	30	0	50	50	0	*	100	150	0	1	1	1	0	0	0	200	0	100	100	0	0	1	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	30	0	16	10
DSTE53	0	0	1	10	0	0	3	1	1	0	0	0	0	1	10	0	50	50	0	5	150	150	0	2	1	1	0	0	0	200	0	75	75	0	0	1	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	30	0	16	5
DLIN54	0	0	1	4	0	0	3	1	1	0	0	0	0	2	50	0	100	100	0	5	100	200	0	1	1	1	0	0	0	300	0	100	100	0	0	1	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	20	0	14	5
DCRU55	0	0	1	4	0	0	3	1	1	0	0	0	0	1	25	0	50	50	0	5	100	150	0	1	1	1	0	0	0	100	0	50	50	0	0	1	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	2	2	2	40	0	20	3
DQUA56	0	1	1	4	0	0	1	1	1	0	0	0	0	1	20	0	50	50	0	5	150	200	0	1	1	1	0	0	0	200	0	100	100	*	*	*	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	2	2	2	60	0	20	5

Appendix 2 cont.

DTSI57	0	0	1	3	0	0	3	0	0	0	0	0	0	1	20	0	100	100	0	10	100	*	0	*	1	1	0	0	0	100	0	75	75	0	1	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	*	1	0	0	0	0	0	0	*	0	*	*
DFAL58	0	1	1	3	0	0	1	0	1	0	0	0	0	1	15	0	50	50	0	5	100	*	0	*	1	1	0	0	0	150	0	50	100	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	2	2	2	27	0	20	5
DSZE59	0	0	1	4	0	0	3	0	1	0	0	0	0	1	30	0	50	50	0	10	100	*	0	1	1	1	0	0	0	150	0	50	50	*	*	*	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	2	2	1	15	0	50	10
DFAU60	0	0	1	5	0	0	3	1	1	0	0	0	0	1	15	0	50	50	0	*	75	100	0	0	1	1	0	0	0	100	0	50	50	*	*	*	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	24	0	30	5
DKOE61	0	0	1	3	0	0	0	0	0	0	0	0	0	1	10	0	50	50	0	5	100	100	0	1	1	1	0	0	0	150	0	50	50	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	15	0	14	0
DGRA62	0	0	1	10	0	0	3	0	0	0	0	0	0	1	20	0	50	50	0	10	100	100	0	1	1	1	0	0	0	150	0	25	25	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	50	0	8	0
DLYT63	0	0	1	4	0	0	3	0	1	0	0	0	0	1	15	0	50	50	0	5	100	*	0	*	1	1	0	0	0	250	0	100	100	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	10	0	12	5
DPUM64	0	0	1	4	0	0	3	0	1	0	0	0	0	1	25	0	50	50	0	5	50	100	0	1	1	1	0	0	0	150	0	100	100	0	0	1	0	0	0	0	0	*	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	10	0	12	0
DMAR65	0	6	0	*	0	1	1	0	1	0	0	0	0	1	60	1	200	100	0	10	100	200	0	1	1	1	0	0	1	200	0	50	100	1	0	0	0	0	0	0	0	*	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	2	15	0	20	10
DAND66	0	0	0	*	0	1	3	2	1	0	0	0	0	1	35	0	50	50	0	5	100	150	0	1	1	1	0	0	0	150	0	50	50	0	0	1	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	2	2	2	10	0	12	5
DGLA67	0	5	0	*	0	1	0	0	1	0	1	0	0	2	15	0	50	50	0	5	100	100	0	0	0	0	0	0	0	150	0	50	50	0	0	1	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	45	0	50	0
DAUR68	0	10	0	*	0	1	0	1	2	0	1	0	0	1	30	0	50	50	0	5	100	125	0	0	1	1	0	0	0	200	0	75	75	1	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	70	0	30	0
DSAL69	0	10	0	*	0	0	0	0	1	0	0	0	0	1	30	0	50	50	0	5	50	125	0	1	1	1	0	0	0	125	0	75	75	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	35	0	6	10
DRUG70	0	1	0	*	0	1	0	0	1	0	1	0	0	1	15	0	30	30	0	5	100	100	0	1	1	1	0	0	0	150	0	100	100	*	*	*	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	2	2	2	30	0	20	5
DMYO71	0	2	0	*	0	1	0	0	1	0	1	0	0	1	10	0	30	30	0	5	50	100	0	1	1	1	0	0	0	100	0	50	50	*	*	*	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	2	2	2	70	0	20	5
PBEN72	0	30	0	*	0	1	0	1	2	0	1	0	0	2	60	0	100	100	0	5	250	300	0	1	1	1	0	0	0	500	0	300	200	1	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	6	1	30	5
PPAR73	0	35	0	*	0	1	0	1	2	0	1	0	0	2	50	0	100	100	0	5	300	300	0	1	1	1	0	0	0	500	0	300	150	1	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	6	1	20	5
PPAN74	0	30	0	*	1	1	1	1	2	0	1	0	0	2	60	0	150	150	0	5	300	300	0	1	1	1	0	0	0	500	0	100	100	*	*	*	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	2	1	1	10	1	30	0
PTUB75	0	20	0	*	0	1	1	1	2	0	1	0	0	2	25	0	100	100	0	10	250	*	0	*	1	1	*	0	0	500	0	150	150	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	*	*	*	*	1	0	0	1	1	1	1	15	1	24	10
PGLA76	0	40	0	*	0	1	0	1	2	0	1	0	0	2	20	0	150	150	0	10	300	300	0	1	1	1	0	0	0	400	0	150	150	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	15	0	50	0
PHEY77	0	40	0	*	0	1	1	0	2	0	1	0	0	2	40	0	150	150	0	5	250	300	0	1	1	1	0	0	0	400	0	200	100	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	15	1	30	0
PCAB78	0	40	0	*	0	1	0	0	2	0	1	0	0	2	40	0	200	200	0	5	300	300	0	1	1	1	0	0	0	300	0	200	100	0	0	1	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	2	2	2	15	1	20	5
PELS79	0	10	0	*	0	1	1	1	1	0	0	0	0	2	30	0	100	100	0	5	400	400	0	1	1	1	0	0	0	500	0	200	100	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	30	1	28	10
PAMA80	0	30	0	*	0	1	1	1	2	0	0	0	0	2	15	0	100	100	0	5	200	200	0	0	1	0	0	0	0	200	0	100	100	1	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	15	0	30	0
PFOR81	0	25	0	*	0	1	1	0	2	0	0	0	0	1	20	0	100	100	0	5	250	250	0	1	1	1	0	0	0	300	0	150	100	*	*	*	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	2	12	1	16	0
PMEN82	0	5	0	*	0	1	0	0	1	0	0	0	0	1	20	1	150	100	1	5	100	150	0	1	1	1	0	0	0	300	0	150	125	*	*	*	0	0	0	0	0	*	0	2	0	0	0	0	0	0	0	0	1	1	1	0	0	2	2	2	20	0	16	20
PFRA83	0	30	0	*	0	1	2	1	2	0	0	0	0	1	20	1	200	100	1	10	200	300	0	1	1	1	0	0	0	400	0	250	250	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	20	0	14	20
PBRA84	0	10	0	*	0	1	0	1	2	0	0	0	0	1	15	1	100	50	1	5	200	200	0	1	1	1	0	0	0	300	0	200	200	0	0	1	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	1	1	1	0	0	2	2	2	15	0	12	20

```
PMIC85   0 10 0  * 0 1 0 2 1 0 0 0 0 1 40 0 150 150 0  5 200 200 0 1 1 1 0 0 0 300 0 200 150 0 0 1 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 1 1 1 0 0 0 1 2 10 0 20 10
PMUT86   0  2 0  * 0 1 0 2 1 0 1 0 0 1 30 0 150 150 0  5 200 200 0 1 1 1 0 0 0 300 0 200 150 0 0 1 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 1 1 1 0 0 1 1 2 20 0 20 10
PNIG87   0  4 0  * 0 1 2 2 2 0 0 0 0 1 20 1 200 100 1  5 200 300 0 1 1 1 0 0 0 300 0 100 100 * * * 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 1 1 1 0 0 2 2 2 20 0 20 10
PPHI88   0 20 0  * 0 1 2 1 2 0 0 0 0 1 30 0 200 200 0 10 450 450 0 1 1 1 0 0 0 600 0 400 250 * * * 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 1 1 1 20 0 20 10
PREF89   0 20 0  * 0 1 0 1 2 0 0 0 0 1 20 0 200 200 1 10 400 400 0 1 1 1 0 0 0 600 0 200 150 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 1 1 0 0 2 1 2 20 0 14 20
PRET90   0 70 0  * 0 1 2 1 2 0 0 0 0 1 25 0 100 100 0 10 400     * * * 1 1 0 0 0 600 0 350 250 * * * 0 0 0 0 0 * * 1 0 0 0 0 0 * * * * 1 1 0 0 1 1 1 14 0  8 10
PMOL91   0 10 0  * 0 2 2 2 1 0 0 0 0 1 30 0 120 120 0 10 250 300 0 1 1 1 0 0 0 400 0 200 150 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 1 1 1 0 0 2 2 2 20 0 16 20
PTRA92   0 50 0  * 0 1 0 1 2 0 0 0 0 1 15 0 200 200 0 10 300 300 0 1 1 1 0 0 0 400 0 200 200 * * * 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 1 0 20 0 12 20
PATR93   0 10 0  * 0 1 0 1 2 0 1 0 0 1 20 0 200 200 1 10 500 500 0 1 1 1 0 0 0 600 0 400 300 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 * * * * 1 0 0 0 2 2 2 12 0 16  5
PSPE94   0 60 0  * 0 1 2 2 2 0 1 0 0 1 20 0 200 200 1  5 400 400 0 1 1 1 0 0 0 400 0 300 200 1 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 * * * * 1 1 0 0 1 1 1 30 0 20 10
PVEL95   0 40 0  * 0 1 2 1 2 0 0 0 0 1 30 0 100 100 0 10 400 400 0 1 1 1 0 0 0 500 0 300 200 * * * 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 1 1 0 1 2 2 2 30 0 24 10
PWIL96   0 20 0  * 0 1 0 1 2 0 0 0 0 1 40 0 100 100 0 10 400 400 0 1 1 1 0 0 0 500 0 350 250 * * * 0 0 0 0 0 * 0 1 0 0 0 0 0 * * * * 1 1 0 1 1 2 2 25 0 30 10
PPUR97   0 20 0  * 1 1 0 0 2 0 1 0 0 2 40 0 200 200 0  5 300 400 0 1 1 1 0 0 0 400 0 300 200 * * * 0 0 0 0 0 * 0 2 0 0 0 0 0 0 0 0 1 1 1 0 0 1 1 1 14 1 20  0
PPAL98   0 20 0  * 0 1 2 0 2 0 0 0 0 1 15 1 100  75 0  5   * 300 0 1 1 0 0 0 0 200 0 200 150 * * * 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 1 1 0 0 0 1 1 1 15 0 20 10
PVIL99   0  5 0  * 0 1 0 1 1 0 1 0 0 2 50 0 100 100 0  5 250 250 0 1 1 1 0 0 0 400 0 150 100 0 0 1 0 0 0 0 0 * 0 2 0 0 0 0 0 0 0 0 1 1 0 0 0 2 2 2  6 1 40  0
PWIG100  0 20 0  * 0 1 2 0 2 0 0 0 0 1 20 0 100 100 0  5 400     * * * 1 1 0 0 0 500 0 300 200 * * * 0 0 0 0 0 0 0 1 0 0 0 0 0 * * * * 1 0 0 0 1 1 1 15 0 14 10
PROT101 00  3 0  * 0 1 2 2 1 0 0 0 0 1 30 0 100 100 0 10 200 300 0 1 1 1 0 0 0 250 0 200 200 * * * 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 1 1 0 0 2 2 2 20 0 24 10
PSTR102  0  5 0  * 0 1 0 0 1 0 0 0 0 1 30 1 150 100 0 10 250 300 0 1 1 1 0 0 0 350 0 200 200 0 0 1 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 1 1 0 0 0 1 1 1 30 0 20 10
PHIS103  0 40 0  * 0 1 1 0 2 0 0 0 0 1 35 0 125 125 0  5 300 300 0 1 1 0 0 0 0 300 0 150 125 * * * 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 1 1 0 0 0 1 1 2 10 0 30  0
PPUB104  0 20 0  * 0 1 2 0 2 0 1 0 0 2 25 0 100 100 0  5 300     * * * 1 1 0 0 0 450 0 200 150 * * * 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 1 1 0 0 0 1 1 2 12 1 30  0
PBRE105  0 20 0  * 0 1 0 1 2 0 0 0 0 1 20 0 100 100 0  5   * 150 0 1 1 0 0 0 0   * 0   *   * * * * 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 1 1 0 0 0 1 1 1 12 0 16  5
PNEL106  0 40 0  * 0 1 0 0 2 0 1 0 0 2 60 0 100 100 0  5   * 300 0 0 1 1 0 0 0 300 0 150 150 0 0 1 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 10 1  8  5
PBAT107  0 20 0  * 0 1 0 0 2 0 1 0 0 2 25 0 100 100 0  5 200 300 0 1 1 1 0 0 0 300 0 100 100 0 0 1 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 1 1 1 0 0 1 1 1 10 0 16  5
PWAT108  0 20 0  * 0 1 0 0 2 0 1 0 0 2 30 0 100 100 0  5 200   * 0 1 1 1 0 0 0 250 0 150 100 * * * 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 1 1 0 0 0 1 1 1 10 0 16  0
PHIR109  0 10 0  * 0 1 0 0 1 0 0 0 0 1 10 1 200 200 0 10   * 200 0 1 1 1 0 0 0 300 0 100 100 0 0 1 0 0 0 0 0 * 0 2 0 0 0 * 0 0 0 0 1 1 0 0 0 1 1 1  6 0  6 10
PRUP110  0 10 0  * 0 1 0 0 1 0 0 0 0 1 20 0 100 100 0 10 250 300 0 1 1 1 0 0 0 400 0 150 150 0 0 1 0 0 0 0 0 2 0 2 0 0 0 0 0 0 0 0 1 1 0 0 0 1 1 1 10 0 80  5
PMAC111  0 30 0  * 0 1 0 0 2 0 0 0 0 1 30 0 200 200 0  5 300 400 0 1 1 1 0 0 0 300 0 300 200 * * * 0 0 0 0 0 0 0 2 0 0 0 0 0 * * * 1 1 0 0 0 1 1 1 20 0 20 10
PGAR112  0 30 0  * 1 1 0 0 2 0 1 0 0 2 50 0 100 100 0  5 250 300 0 1 1 1 0 0 0 250 0 150 100 0 0 1 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 1 1 0 0 0 1 1 1 16 1 30  0
```

Appendix 2 cont.

PCHA113	0	20	0	*	0	1	0	0	1	0	1	0	0	2	25	0	100	100	0	5	250	300	0	1	1	1	0	0	0	300	0	200	200	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	10	1	20	0
PDIE114	0	10	0	*	0	1	1	1	2	0	1	0	0	2	20	0	100	100	0	5	300	*	0	0	1	1	0	0	0	500	0	200	100	0	0	1	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	15	1	24	10
PGRI115	0	10	0	*	0	1	0	1	1	0	1	0	0	2	25	0	150	150	0	10	200	250	0	1	1	1	0	0	0	400	0	200	150	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	2	12	1	24	0
PNIL116	0	10	0	*	0	0	0	2	1	0	1	0	0	1	50	0	150	150	0	10	*	300	0	1	1	1	0	0	0	400	0	200	200	*	*	*	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	2	2	2	30	0	20	10
PLIT117	0	20	0	*	0	1	0	0	2	0	0	0	0	1	30	1	300	150	1	10	300	400	0	2	1	1	0	0	0	250	1	100	100	0	0	1	0	0	0	0	0	2	0	2	0	0	1	0	0	0	0	0	1	1	1	0	0	1	1	1	15	0	16	30
RDEP118	0	3	0	*	0	1	0	0	1	1	2	0	1	2	50	0	100	100	0	10	300	300	0	1	1	1	0	0	0	500	0	100	200	0	0	1	2	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	0	1	0	1	1	1	40	0	20	10
RSIN119	0	4	0	*	0	1	0	1	1	1	2	0	1	2	50	1	200	125	0	*	300	*	0	1	1	1	0	0	0	500	0	200	250	0	0	1	2	1	0	0	0	0	0	0	1	*	0	0	0	1	0	*	1	1	0	1	0	2	1	2	40	0	12	10
CFOR120	0	10	0	*	0	1	1	1	1	1	2	0	1	1	30	0	150	150	0	12	400	600	0	1	1	1	0	0	1	900	0	200	400	*	*	*	1	0	0	0	0	1	0	0	0	0	0	0	*	1	0	0	1	1	0	1	0	1	1	2	25	0	14	20
CSTE121	0	20		*	0	1	0	1	1	1	2	0	1	1	50	0	50	50	0	12	300	400	0	1	1	1	0	0	1	600	0	75	100	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	1	1	20	0	8	10
CBAR122	0	5	0	*	0	1	0	1	1	1	2	0	1	1	*	0	50	50	0	12	300	400	0	1	1	1	0	0	1	600	0	100	200	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	1	1	30	0	8	10
CSUB123	0	10	0	*	0	1	0	1	1	1	2	0	1	1	20	0	50	50	0	12	300	*	0	1	1	1	0	0	1	500	0	100	200	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	1	1	45	0	8	10
CJAP124	0	10	0	*	0	1	0	1	1	1	2	0	1	1	35	0	50	50	0	12	300	400	0	1	1	1	0	0	1	550	0	100	200	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	1	1	45	0	8	10
CNIN125	0	5	0	*	0	1	0	1	1	1	2	0	1	1	15	0	100	100	0	15	300	*	0	*	1	1	0	0	1	400	0	100	250	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	1	1	20	0	16	20
CNAN126	0	5	0	*	0	1	1	0	1	1	2	0	1	0	*	0	100	100	0	15	400	*	0	*	1	1	0	0	1	500	0	100	200	0	0	1	2	1	0	0	0	2	0	0	0	0	0	0	*	0	0	0	*	1	0	1	0	1	0	2	20	0	8	20
LCAN127	0	30	0	*	0	1	1	1	1	1	2	0	1	1	25	0	100	100	0	12	400	400	0	1	1	1	0	0	1	700	0	50	300	1	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	1	0	1	0	2	1	2	45	0	16	25
LPLE128	0	3	0	*	0	1	1	0	1	0	1	0	0	2	*30	0	150	150	0	10	100	200	0	1	1	1	0	0	1	400	0	100	150	0	1	0	2	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	1	0	1	0	2	2	2	30	0	24	20
TGOU129	0	10	0	*	0	1	2	2	2	1	2	0	0	0	*	1	100	75	0	5	150	200	0	1	1	1	0	0	1	200	0	200	300	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	1	1	1	0	0	2	2	2	30	0	6	0
THIL130	0	10	0	*	0	1	2	2	1	1	2	0	0	0	*	1	50	25	0	5	50	100	0	1	1	1	0	0	1	50	0	100	150	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	1	1	1	1	0	2	2	2	30	0	8	0
TFRU131	0	15	0	*	0	1	2	2	1	1	2	0	0	0	*	1	50	10	0	5	50	100	0	1	1	1	0	0	1	100	0	125	150	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	1	1	1	1	0	2	2	2	20	0	8	0
KJAP132	0	10	0	*	0	1	0	1	1	0	1	0	0	0	*	1	300	150	1	5	150	300	0	1	0	1	0	0	1	600	0	150	250	1	0	0	1	0	0	0	0	1	2	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	14	2	2	30
KELS133	0	65	0	*	0	1	0	0	1	0	1	0	0	0	*	1	250	200	1	5	150	*	0	1	1	1	0	0	1	500	0	200	200	*	*	*	1	0	0	0	0	1	2	0	0	0	0	0	1	0	0	0	*	1	0	0	0	1	0	1	35	2	2	20
KGLA134	0	25	0	*	1	1	1	0	1	0	1	0	0	0	*	1	200	100	1	5	100	*	0	1	1	1	0	0	1	400	0	200	200	0	0	1	1	0	0	0	0	1	2	0	0	0	0	0	1	0	0	0	*	1	0	0	0	1	0	1	9	2	2	20
KSIN135	0	15	0	*	0	1	0	1	1	0	1	0	0	0	*	1	200	175	1	10	100	*	0	1	1	1	0	0	1	250	0	100	200	1	0	0	1	0	0	0	0	1	2	0	0	0	0	0	1	0	0	0	*	1	0	0	0	0	1	1	40	2	2	20
KSZE136	0	10	0	*	0	1	0	1	1	0	1	0	0	0	*	1	250	200	1	5	150	*	0	1	1	1	0	0	1	400	0	200	200	0	1	0	1	0	0	0	0	1	2	0	0	0	0	0	1	0	0	0	*	1	0	0	0	1	0	1	16	2	2	15
CTER137	0	6	0	*	0	1	1	1	1	0	0	0	0	2	15	0	100	100	0	5	30	50	1	1	1	0	1	0	0	100	0	30	50	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	2	2	2	20	0	24	0
COPP138	0	20	0	*	0	1	0	1	1	0	0	0	0	2	10	0	25	25	0	5	20	50	1	1	1	0	1	0	1	100	0	25	75	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	2	2	40	0	40	0

Appendix 3. List showing the five nearest neighbours for each OTU with the similarities expressed as percentages

OTU	1		2		3		4		5	
	OTU	%	OTU	%	OTU	%	OTU	%	OTU	%
1	65	81.5	34	81.1	32	79.8	38	79.6	102	79.5
2	102	87.1	83	85.6	109	85.6	88	85.3	33	84.9
3	4	97.3	12	94.0	7	91.8	5	91.6	6	91.3
4	3	97.3	12	92.0	7	91.4	5	91.2	6	90.9
5	6	97.4	7	97.3	12	96.9	11	96.3	13	96.0
6	7	98.5	5	97.4	12	97.2	13	96.5	11	95.4
7	6	98.5	5	97.3	13	97.0	12	96.7	9	95.6
8	65	88.5	35	88.3	38	85.9	36	85.5	6	85.5
9	7	95.6	5	95.5	6	94.8	13	94.3	11	93.3
10	16	85.7	12	84.8	15	83.9	6	83.8	7	82.6
11	5	96.3	6	95.4	7	95.3	12	93.7	13	93.7
12	6	97.2	5	96.9	6	96.7	13	94.7	3	94.0
13	7	97.0	6	96.5	5	96.0	12	94.7	9	94.3
14	6	90.7	5	90.7	7	90.6	12	90.0	17	89.6
15	16	96.7	17	88.1	7	84.2	5	84.0	10	83.9
16	15	96.7	17	90.1	6	86.5	7	86.0	10	85.7
17	5	92.4	6	92.1	11	91.8	7	91.8	13	91.0
18	17	87.3	5	87.3	7	86.5	6	86.2	3	84.9
19	20	90.7	34	83.9	20	83.4	39	83.3	65	82.6
20	19	90.7	21	88.4	34	85.6	4	85.2	3	84.0
21	20	88.4	6	86.3	5	86.2	12	85.4	33	85.2
22	52	90.7	51	88.6	60	88.6	63	88.4	64	88.4
23	33	84.1	38	82.3	30	82.1	31	81.5	25	80.5
24	34	86.7	26	86.1	35	85.8	32	85.2	3	84.7
25	105	85.7	35	84.7	38	84.4	92	83.8	80	83.6
26	35	91.3	42	92.0	30	89.8	34	88.4	36	87.9
27	31	89.9	32	88.2	33	88.1	28	87.5	30	86.4
28	30	87.9	27	87.5	26	86.4	14	85.0	31	85.0
29	40	87.8	42	86.4	36	85.8	38	85.6	30	84.6
30	32	92.2	36	92.2	39	92.0	33	91.2	31	91.6
31	32	95.2	33	93.3	34	92.6	30	91.6	41	91.2
32	31	95.2	33	94.5	34	92.8	30	92.2	36	90.7
33	32	94.5	31	93.3	30	91.8	39	90.5	36	89.8
34	32	92.8	31	92.6	35	92.4	30	91.6	38	90.1
35	36	95.0	38	94.8	34	92.4	26	91.3	65	90.5

Appendix 3 cont.

OTU	1		2		3		4		5	
	OTU	%	OTU	%	OTU	%	OTU	%	OTU	%
36	38	96.0	35	95.0	30	92.2	32	90.7	37	90.5
37	38	92.8	40	90.8	36	90.5	65	89.8	35	89.2
38	36	96.0	35	94.8	40	93.4	37	92.8	30	91.3
39	30	92.0	33	90.5	34	88.9	32	88.5	36	87.8
40	38	93.4	37	90.8	35	90.3	36	90.1	29	87.8
41	31	91.2	38	89.6	33	88.6	32	88.4	35	87.3
42	26	91.0	35	87.9	128	87.7	34	87.5	32	87.2
43	45	90.6	54	90.5	85	90.4	61	90.2	69	90.1
44	63	93.5	64	93.5	51	91.3	49	90.5	60	89.5
45	62	95.4	61	93.7	64	92.9	53	91.8	49	91.5
46	50	95.1	47	93.0	49	92.4	60	92.3	63	90.5
47	46	93.0	50	90.1	57	89.9	45	89.6	62	89.5
48	51	94.0	64	93.0	49	92.9	52	92.8	63	91.6
49	51	97.3	64	95.4	63	95.2	52	95.0	60	94.1
50	46	95.1	49	93.6	60	92.8	52	91.7	63	91.1
51	49	97.3	64	97.1	63	96.7	52	96.4	60	94.9
52	64	96.8	51	96.4	63	95.4	49	95.0	53	94.2
53	52	94.2	60	93.0	55	92.6	63	92.5	45	91.8
54	55	91.7	51	91.4	52	90.8	43	90.5	53	90.4
55	56	95.4	58	94.1	66	93.9	59	93.2	53	92.6
56	58	96.9	55	95.4	59	92.0	51	91.1	61	91.1
57	60	92.0	49	91.6	63	90.7	51	90.6	64	90.6
58	56	96.9	59	94.6	55	94.1	61	93.0	59	92.9
59	58	94.6	55	93.2	62	93.2	63	92.7	64	92.7
60	63	95.7	51	94.9	49	94.1	52	93.8	64	93.7
61	62	96.3	69	94.6	45	93.7	58	93.0	49	92.8
62	61	96.3	45	95.4	59	93.2	49	93.0	64	92.6
63	64	99.1	51	96.7	60	95.7	52	95.4	49	95.2
64	63	99.1	51	97.1	52	96.8	49	95.4	60	93.7
65	38	90.8	35	90.5	37	89.8	36	89.2	8	88.5
66	55	93.9	90	91.5	78	90.5	58	90.3	43	90.1
67	44	86.0	106	84.6	70	83.7	71	83.5	68	83.1
68	108	91.3	105	91.1	71	89.2	72	89.0	73	88.8
69	61	94.6	70	92.5	58	92.5	62	92.4	64	92.4
70	71	98.3	58	92.9	69	92.5	66	91.5	86	91.2

OTU	1		2		3		4		5	
	OTU	%	OTU	%	OTU	%	OTU	%	OTU	%
71	70	98.3	69	91.8	58	91.4	66	90.5	56	90.1
72	73	98.8	108	93.5	112	93.4	113	93.1	77	92.7
73	72	98.8	108	93.7	112	93.1	113	92.9	76	92.7
74	77	94.5	112	94.1	72	92.4	73	91.9	75	91.8
75	114	93.4	77	93.1	79	92.6	115	92.2	73	92.0
76	73	92.7	72	92.4	104	91.6	108	90.9	115	90.9
77	112	95.2	74	94.5	113	94.4	108	94.1	75	93.1
78	77	92.9	99	92.8	112	91.7	113	91.3	108	90.7
79	75	92.6	114	92.5	113	92.2	115	92.2	77	91.8
80	105	89.9	108	86.8	98	86.7	114	86.3	113	85.8
81	103	93.4	77	92.1	110	91.2	114	91.0	78	90.5
82	84	94.7	87	93.2	102	90.9	70	90.2	109	90.2
83	87	92.8	90	91.2	84	91.1	81	90.7	88	89.6
84	82	94.7	87	92.2	83	91.1	89	89.4	86	87.0
85	86	95.4	43	90.4	101	89.6	102	89.3	82	88.4
86	83	95.4	116	92.4	107	91.8	115	91.5	70	91.2
87	82	93.2	83	92.8	84	92.2	101	90.6	86	88.6
88	90	94.5	100	93.9	92	92.7	89	91.3	95	91.3
89	93	92.6	88	91.3	92	91.3	96	90.9	83	90.7
90	88	94.9	85	93.7	100	93.6	96	92.6	83	91.2
91	101	94.8	116	91.1	86	87.9	87	87.2	85	86.7
92	88	92.7	89	91.3	111	90.9	90	90.1	105	89.7
93	89	92.8	88	91.2	94	88.4	96	88.3	92	87.4
94	90	90.9	88	90.2	89	90.1	100	89.5	83	89.1
95	96	96.2	90	93.7	101	92.2	88	91.3	89	90.7
96	95	96.2	90	92.6	89	90.9	88	90.7	101	89.1
97	104	91.6	112	91.5	108	91.3	73	90.6	72	90.5
98	105	93.3	100	92.2	111	91.4	103	89.9	108	89.4
99	115	95.1	113	93.6	78	92.8	72	92.1	72	91.9
100	88	93.9	90	93.6	111	93.0	98	92.2	105	90.8
101	91	94.8	95	92.2	86	91.1	87	90.6	85	89.6
102	109	96.1	110	93.8	111	93.1	69	92.1	113	91.0
103	81	93.4	105	93.1	111	92.3	77	91.6	108	90.6
104	108	94.1	72	92.3	73	92.3	77	92.3	113	91.8
105	98	93.3	103	93.1	111	93.0	108	92.1	68	91.1

OTU	1		2		3		4		5	
	OTU	%	OTU	%	OTU	%	OTU	%	OTU	%
106	107	90.9	112	89.5	113	88.9	77	88.5	108	88.4
107	108	97.6	113	94.0	112	93.3	77	92.4	86	91.8
108	107	97.6	113	95.5	112	95.2	77	94.1	104	94.1
109	112	96.1	110	93.8	69	91.6	111	91.2	82	90.2
110	102	93.8	108	93.8	81	91.2	69	90.5	113	90.5
111	102	93.1	100	93.0	105	93.0	108	92.6	103	92.3
112	77	95.2	108	95.2	113	94.9	74	94.1	72	93.4
113	108	95.5	115	95.1	112	94.9	77	94.4	107	94.0
114	75	93.4	79	92.5	77	92.3	73	91.1	74	91.0
115	99	95.1	113	95.1	75	92.2	79	92.2	77	92.0
116	86	92.4	91	91.1	70	90.6	102	89.5	101	89.4
117	83	86.3	82	86.1	109	86.0	102	84.4	84	84.0
118	119	94.8	126	83.6	125	83.4	124	82.1	122	81.8
119	118	94.8	125	83.9	120	82.7	126	81.6	124	81.4
120	125	93.5	122	89.4	124	89.4	123	89.2	121	88.4
121	124	97.7	123	97.7	122	95.7	125	92.3	120	88.4
122	123	96.1	124	95.9	121	95.7	125	93.7	120	89.4
123	124	99.2	121	97.7	122	96.1	125	93.4	120	89.2
124	123	99.2	121	97.9	122	95.9	125	93.2	120	89.4
125	122	93.7	120	93.5	123	93.4	124	93.2	121	92.3
126	123	85.1	120	85.1	118	83.6	119	81.6	7	80.5
127	124	85.7	123	85.2	122	85.0	121	84.3	120	84.2
128	42	87.7	29	84.1	24	84.1	26	83.5	39	83.5
129	130	94.1	131	92.2	101	79.6	13	79.4	12	79.3
130	131	97.7	129	94.1	24	79.9	13	79.1	40	79.1
131	130	97.7	129	92.2	13	81.0	12	80.9	6	80.0
132	135	94.0	133	89.7	136	88.7	134	83.0	25	80.1
133	136	96.0	135	93.7	134	93.3	132	89.7	7	83.0
134	133	93.3	136	89.5	135	87.7	5	86.4	7	85.7
135	132	94.0	133	93.7	136	92.7	134	87.7	8	82.1
136	133	96.0	135	92.7	134	89.5	132	88.7	14	84.5
137	138	95.2	105	79.8	80	79.4	33	78.7	36	77.3
138	137	95.2	105	80.5	71	77.9	70	77.8	74	77.7

Appendix 4. Distribution of OTUs in the six and nine group schemes for clustering to maximize WGMS analysis

Six group scheme

Group 1.
66 : 70 : 71 : 82 : 84 : 85 :
86 : 87 : 91 : 98 :101 :102 :
103 :105 :109 :110 :111 :116 :
137 :138.

Group 2.
68 : 72 : 73 : 74 : 75 : 76 :
77 : 78 : 79 : 80 : 81 : 97 :
99 :103 :106 :107 :108 :112 :
113 :114 :115.

Group 3.
1 : 2 : 3 : 4 : 5 : 6 :
7 : 8 : 9 : 10 : 11 : 12 :
13 : 14 : 15 : 16 : 17 : 18 :
19 : 20 : 21 : 23 : 24 : 25 :
26 : 27 : 28 : 29 : 30 : 31 :
32 : 33 : 34 : 35 : 36 : 37 :
38 : 39 : 40 : 41 : 42 : 65 :
128 :129 :130 :131 :132 :133 :
134 :135 :136.

Group 4.
118 :119 :120 :121 :122 :123 :
124 :125 :126 :127.

Group 5.
83 : 88 : 89 : 90 : 92 : 93 :
94 : 95 : 96 :100 :117.

Group 6.
22 : 43 : 44 : 45 : 46 : 47 :
48 : 49 : 50 : 51 : 52 : 53 :
54 : 55 : 56 : 57 : 58 : 59 :
60 : 61 : 62 : 63 : 64 : 67 :
69.

Nine group scheme

Group 1.
118 :119 :120 :121 :122 :123 :
124 :125 :126 :127.

Group 2.
132 :133 :134 :135 :136.

Group 3.
126 :130 :131.

Group 4.
22 : 43 : 44 : 45 : 46 : 47 :
48 : 49 : 50 : 51 : 52 : 53 :
54 : 55 : 56 : 57 : 58 : 59 :
60 : 61 : 62 : 63 : 64 : 65 :
69.

Group 5.
70 : 71 : 82 : 83 : 84 : 85 :
86 : 87 : 88 : 89 : 90 : 91 :
92 : 93 : 94 : 95 : 96 : 98 :
100 :101 :102 :103 :105 :109 :
110 :111 :116 :117.

Group 6.
1 : 2 : 8 : 19 : 23 : 24 :
25 : 26 : 27 : 28 : 29 : 30 :
31 : 32 : 33 : 34 : 35 : 36 :
37 : 38 : 39 : 40 : 41 : 42 :
65 :128.

Group 7.
68 : 72 : 73 : 74 : 75 : 76 :
77 : 78 : 79 : 80 : 97 : 99 :
103 :106 :107 :108 :112 :113 :
114 :115.

Group 8.
67 : 80 :137 :138.

Group 9.
3 : 4 : 5 : 6 : 7 : 9 :
10 : 11 : 12 : 13 : 14 : 15 :
16 : 17 : 18 : 20 : 21.

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Synopsis

William Hudson (1734–1793) was the earliest English botanist to adopt the Linnaean systems of classification and nomenclature. The two editions of *Flora anglica* are of special significance to phycologists because both contain numerous descriptions of new species of algae; in other groups of plants (except lichens) these are very few. The algal descriptions given by Hudson are imprecise by modern standards, but his taxonomic views can often be interpreted by critical typification of the names of his new taxa. This requires an understanding both of the materials Hudson used and of his philosophy and method of work. Although these were not stated explicitly by Hudson, they can to some extent be deduced even 200 years after publication, as indicated here. A selection of nine species from amongst those described by Hudson provides a series of examples illustrating the problems to be dealt with in the typification of Hudson's algal names.

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1. Introduction

William Hudson (1734–1793) was the earliest English botanist to adopt the Linnaean systems of classification and nomenclature. The two editions of *Flora anglica* (Hudson, 1762; 1778) are of special significance to phycologists because both contain numerous new species of algae, whereas for other groups of plants (except lichens) these are relatively few. The posthumous, so-called third, edition (Hudson, 1798) is identical to the second edition, except for the correction of some printer's errors. In the course of preparing the various checklists of British marine algae (see Parke & Dixon, 1976) and *Seaweeds of the British Isles* (Dixon & Irvine, 1977*a*), the significance of Hudson's works showed repeatedly. Thus, in the current *Check-list of British marine algae—third revision* (Parke & Dixon, 1976), 37 species of Rhodophyta, Phaeophyta and Chlorophyta have Hudsonian basionyms. Some of them, and other names now reduced to synonymy, have already been considered (Dixon, 1959*b*, 1960, 1962, 1963, 1967; Dixon & Irvine, 1977*a, b*), and Laundon (1963, 1966, 1976) has typified three Hudson lichen names. We eventually realized, however, that this piecemeal approach was unsatisfactory, and that a more comprehensive study was desirable.

The algal descriptions given by early authors such as Hudson are imprecise by modern standards, so that critical typification of the names of new taxa is imperative. This requires an understanding of the materials used and also of the author's philosophy and method of work which were not stated explicitly, but can to some extent be deduced even 200 years after publication. In the case of Hudson, a resumé of his life and of the history of his personal herbarium has been previously presented (Dixon, 1959*a*).

Herbaria are cited by their official abbreviations:

BAS:	Botanisches Institut der Universität Basel, Switzerland.
BM:	British Museum (Natural History), London.
BM-K:	Specimens formerly in the Herbarium of the Royal Botanic Gardens, Kew, and now at the British Museum (Natural History), London.
BM-SL:	The Sloane Herbarium at the British Museum (Natural History), London.
K:	The Herbarium, Royal Botanic Gardens, Kew.
LINN:	Linnean Society of London.
NMW:	National Museum of Wales, Cardiff.
OXF:	Fielding-Druce Herbaria, The University, Oxford. For details of the Morison, Ray and Dillenius herbaria, see Clokie (1964).

2. Hudson's species concept

The algae of *Flora anglica*: first edition

Hudson's species concept was obviously derived directly from that of Linnaeus, for which Stearn (1957) has given a detailed exposition. This close relationship means that the mechanics involved in the typification of Hudson's species are similar to the Linnaean examples discussed by Stearn. The similarity is particularly noteworthy in the first edition of *Flora anglica* where 49% of the algal binomials were taken from the first edition of *Species plantarum* (Linnaeus, 1753), with the remainder newly described.

The sources which Hudson used in the preparation of his algal descriptions for the first edition of *Flora anglica* fall into three categories, used singly or in combination, as follows:

1. Herbarium specimens which were originally in his possession

From the comments made and additional information provided by Hudson in his species' treatments, it is clear that he must have had specimens of his own, although it may be difficult to find these at the present time. It was common for botanists of that period to replace a specimen (even one which had been used for a description) with another which was considered to be more appropriate, but not necessarily conspecific by modern standards. Secondly, Hudson's possessions were largely destroyed by fire in 1783 and it is not known with any certainty what parts (if any) of his early herbarium survived. The dispersal of herbarium material which once belonged to Hudson was chronicled by Dixon (1959*a*), who showed that about 200 specimens were then located at BM and K. The algal collections at the latter have now been transferred to the former (see Ross & Brenan, 1970).

The algal herbarium of Hudson's contemporary, Lightfoot, which contains many specimens received from Sir Thomas Frankland said to have been identified by Hudson, was eventually found in an attic at Saffron Walden Museum (Dixon, 1959*a*). It is now on permanent loan to K and has been transferred with other algal material to BM. The folder, once the property of Frankland, containing algal specimens, mentioned by Dixon (1959*a*) as being at LINN, has also been transferred to BM. Thus, at present, virtually all known Hudson material is preserved at BM but it is always possible that some authentic Hudson specimens, even types, remain undetected and may come to light in obscure places.

2. Other herbarium specimens quoted by Hudson

Three collections of particular relevance to Hudson algal binomials are those of Buddle, Petiver and Plukenet. These are all now in the Sloane Herbarium (BM-SL), of which Dandy (1958) has given a detailed account, and were probably consulted by Hudson when he was employed as a resident sublibrarian at the British Museum between 1757 and 1758. Buddle and Petiver were two of the most famous plant collectors of the early 18th century who corresponded and exchanged specimens with many other botanists. Their herbaria were acquired by Sir Hans Sloane in 1715 and 1718, respectively, and became part of the national collections on the death of the latter in 1753. Although Hudson made direct reference to material from these collections only infrequently, the herbaria are of great importance because they had previously been used extensively by Ray (1724) and Dillenius (1742). Knowledge of these collections enabled Hudson to interpret the two pre-Linnaean authors better than any other botanist.

3. Previously-published descriptions and illustrations

Unlike many of his contemporaries, Hudson obviously considered illustrations of particular importance when he was interpreting a previous description, so that these were quoted whenever possible. The illustrations cited most frequently in the first edition of *Flora anglica* (Hudson, 1762) are those by Morison (1680–99), Ray (1724), and Dillenius (1742), although there is no evidence that Hudson ever consulted their herbaria at Oxford (OXF). The third edition of Ray's *Synopsis* was prepared anonymously by Dillenius and published after Ray's death. Hudson's citation *R. Syn.* refers to this edition.

The three genera *Fucus, Ulva* and *Conferva* contain 91 algal species in Hudson's first edition. Of these, 45 are species described previously by Linnaeus, 13 are new species based entirely on his own herbarium material while 33 are new species based on specimens, illustrations or descriptions by pre-Linnaean authors, sometimes in combination with Hudson's own herbarium material and sometimes not.

The algae of *Flora anglica*: second edition

In the second edition of *Flora anglica* (Hudson, 1778), Linnaeus was still by far the most frequently-quoted author. Here the second edition of *Species plantarum* (Linnaeus, 1763) was a major source, although other Linnaean publications were also used (e.g. Linnaeus, 1753, 1767, 1771, 1774) and, in addition, Hudson occasionally quoted other phycological works (Ellis, 1767; Gmelin, 1768; Oeder, 1762–1883).

Analysis of the second edition is more difficult as the species treated do not fit into categories as neatly as for the first edition, reflecting the increasing complexity of phycology between 1762 and 1778. In the second edition 141 algal species are treated in the same three genera mentioned previously, 72 species being carried over from the first edition. Of the 62 species which occur for the first time, eight are species described previously by Linnaeus (in 1753 or later), four are based on previous treatments by Gmelin (1768), and two are based on treatments by Ellis (1767). New species based entirely on Hudson's own material total 29, while 16 new species are based on entities described by pre-Linnean authors, sometimes in combination with his own material and sometimes not. A few species from the second edition which cannot be characterized are omitted from this analysis.

The two editions differ, therefore, in the number of algal species treated, with a more than 50% increase in the second edition over the first. The actual treatment of a particular species in the two editions of *Flora anglica* may differ in various ways, often subtle. A point frequently overlooked by subsequent workers is that, for both Hudson and Linnaeus, the nomenclatural system which they used differed from current practice in two principal ways.

The first difference is in relation to the use of binomials. These are usually regarded as a revolutionary advance made by Linnaeus in 1753, whereas, as Stearn (1957) has indicated, they were introduced primarily as 'an indexer's paper-saving device'. Although the polynomials of previous authors were cumbersome, investigators still *thought* in such terms even after Linnaeus's introduction of binomials. As a consequence, Hudson cites synonyms exclusively in polynomial form in the first edition. Ellis (1767) and Gmelin (1768) were the first phycologists to accentuate binomials, the latter probably having the greater influence through the typographic device of heading each species treatment with a binomial in bold type and relegating polynomial synonyms to a minor position. This is in marked contrast to the procedures of Linnaeus and Hudson, where the specific epithet is merely a marginal annotation to a polynomial beginning with the generic name. Thinking in terms of binomials probably had a great effect on stability; polynomials could be constantly modified, an open invitation to transfer of application. Binomial synonyms began to appear in Hudson's second edition, with references to Ellis (1767) and Gmelin (1768).

Secondly, the basic principle two centuries ago was that the more recent version of a text was the more definitive. Because the later publication was considered to be superior to the earlier work ('altera, emendata et aucta'), the second edition rarely refers back to the first. In a very few cases species were placed in synonymy by citation of an additional marginal epithet, although a few more were given as page references to polynomials. It was much later that de Candolle (1867) first stressed the principle of priority, which led to the formulation of a nomenclatural code. Thus, changes introduced by Hudson in an effort to improve had a significance to him different from that of current nomenclatural practice.

The changes between the two editions are of several kinds:

1. modifications in the polynomial description of a species, including substitution of words or phrases;
2. deletion, addition or transfer of synonyms (particularly pre-Linnaean polynomials), always without explanation;
3. changes of epithet, usually without explanation, but apparently done in most cases because one epithet was considered more appropriate than another;
4. changes in the anglicized 'common name'.

Casual inspection of the two editions did not reveal some of these changes; they became apparent only after making detailed comparisons of all the species treated. It is interesting to consider them in the light of the comments made above, for they were obviously regarded by Hudson as improvements.

3. The typification process

Historical comments

By definition (Stafleu *et al.*, 1978), a nomenclatural type is that element to which the name of a taxon is permanently attached. A holotype is the original single specimen or other element used by the author, whereas the lectotype is a specimen or other element selected later from a group of original materials. For recently-described taxa, the type must be indicated for the name to be validly published. Prior to 1958 this requirement did not apply, and it is necessary to establish the types and their status. For earlier authors this is not always easy, and there are several serious problems involved with Hudson's algal names because of the changes in treatment between the editions. These may reflect improved knowledge or they may represent a real change in

Hudson's taxonomic opinion and therefore in the application of an epithet. Of the materials which he used, specimens in the Sloane Herbarium (BM-SL) are still largely as they were when they were examined by Hudson. The situation with his own herbarium materials is much less satisfactory, however, and almost without exception specimens have been remounted and/or relabelled, probably eliminating much information which would be fundamental to the present study. Because of this, it is not clear whether any extant specimen was used as the basis for a diagnosis in either edition or represents a superior specimen, substituted later.

Procedure adopted

The basic procedure adopted in the typifications of the Hudson binomials presented here and elsewhere (e.g. Dixon, 1967) has been to analyse the descriptions and treatments of the two editions in their entirety and to identify the source material(s) used by Hudson for each entity. At the same time, complete searches of herbaria (BM, BM-K, BM-SL, etc.) were made to provide catalogues of all material now existing which was alleged to have been in Hudson's possession and to locate all materials to which he made reference, or which Frankland said Hudson had identified. Integrating these two aspects indicated whether the elements upon which a species had been based were homogeneous or heterogeneous. In addition, further analyses were conducted of other herbaria and publications (Dillwyn, 1802–9; Turner, 1802; Turner, 1808–19; Smith & Sowerby, 1790–1814) to obtain information on contemporary or near-contemporary opinion.

Where it is clear that Hudson provided no information which might suggest possession of his own herbarium material and that his treatment was based entirely on a single pre-Linnaean illustration, this is the holotype, as in the case of *Fucus scorpioides* (Example Ia).

In other cases one element was a pre-Linnaean specimen or illustration and the other personal herbarium material. Sometimes all pieces of evidence proved to be taxonomically homogeneous both by present-day and near-contemporary standards, so that there were no doubts as to the application of a name. In such cases the pre-Linnaean specimen or illustration was selected as lectotype because of the uncertainties surrounding the surviving Hudson herbarium specimens. Examples of this are *Conferva imbricata* (Example IIa), *Fucus pinnatifidus* (Example IIb), and *F. plumosus* (Example IIc).

The situation became complicated where the data proved to be heterogeneous or where the identity of the pre-Linnaean element was in doubt. The uncertainty over the dates of collection of the surviving Hudson specimens is such that to accept a Hudson specimen as unequivocal lectotype is unwarranted. For cases such as *Conferva elongata* (Example IIIa) and *Fucus plicatus* (Example IIIb), an extant Hudson specimen was therefore assigned the status of *provisional* lectotype.

Finally there remain those cases where Hudson described a species exclusively from his own material and where none of this can be located at the present time. Providing that there had been no disagreement about the application of a name by Hudson's contemporaries and no subsequent deviation in usage, it seemed sensible to retain the epithet and select the original diagnosis as type in the absence of any material. Examples of this procedure are *Conferva fucoides* (Example IVa) and *C. nigra* (Example IVb). In cases where both contemporary and present-day opinion are uncertain about the attribution of a name, as in *C. fulva* (Example Va), typification is clearly not possible.

The Code (Stafleu *et al.*, 1978) makes provision for the selection of neotypes in cases where the original specimens are missing. This procedure is frequently used by lichenologists, and Laundon (1976) adopted it for *Caloplaca flavorubescens* (Huds.) Laundon. Phycologists, on the other hand, seem less prepared to accept neotypes and we have not selected any here. Nevertheless, we would like to suggest that in future neotypes could be used in cases where this would expedite the clarification of the nomenclatural tangles which so often hinder the pursuit of taxonomy.

4. Examples of the typification of Hudson's algal names

These are as follows:

I. Holotype: a pre-Linnaean illustration
    a. *Fucus scorpioides*.
II. Lectotype: a pre-Linnaean illustration
    a. *Conferva imbricata,* b. *Fucus pinnatifidus,* c. *F. plumosus*.
III. Lectotype (provisional): a Hudson specimen
    a. *Conferva elongata,* b. *Fucus plicatus*.
IV. Lectotype: a Hudson description
    a. *Conferva fucoides,* b. *Conferva nigra*.
V. *Species inquirenda*
    a. *Conferva fulva*.

I. Holotype: a pre-Linnaean illustration

EXAMPLE a. *Fucus scorpioides* Huds. [*Bostrychia scorpioides* (Huds.) Mont.]

The original description of *Fucus scorpioides* by Hudson (1762:471) is printed as follows:

> 23. FUCUS caule tereti ramoso, ramis alternis ramosissimis apice inflexis. *scorpioides*
> Fucoides erectum fruticuli specie, summitatibus inflexis. *R. Syn.* 38. *t.* 2. *f.* 6.
> *Anglis*, upright Fucus.
> Habitat *in littore* Sussexiano; *at* Selsey-Island *plentifully*. Dr. Dill. *R. Syn.*

Hudson's treatment was evidently based entirely on the previous treatment and illustration by Dillenius in Ray (1724:38) because the only locality cited by Hudson was taken directly from the latter: 'In the Marshes at *Selsey Island*, Sussex, plentifully'. There is no evidence that Hudson ever examined the Oxford herbaria and he appears to have based his treatment on the Dillenius illustration (Ray, 1724: pl. 2, fig. 6). This illustration is somewhat stylized although there is little doubt that it refers to the alga known today as *Bostrychia scorpioides* (Huds.) Mont. The material on which the illustration was based is in the *Synopsis* herbarium (OXF), and is of that alga (see also Batters in Druce & Vines, 1907:21). The illustration is the holotype of *Fucus scorpioides* Huds.

No material referred by Hudson to his *Fucus scorpioides* has been located in any herbaria. This may well be due to the changes which occurred between the two editions of *Flora anglica*. Gmelin (1768) described *Fucus amphibius* quoting as a synonym the *Fucoides erectum fruticuli* . . . of Ray which Hudson had used as the basis for his *Fucus scorpioides* in the first edition. In the second edition Hudson (1778) referred to Gmelin, accepted Gmelin's binomial and quoted also the *Fucoides erectum fruticuli* . . . of Ray, but made no reference to his own *Fucus scorpioides*. A 'Hudson Sale' specimen of *Bostrychia scorpioides*, which was acquired by BM through the Forster herbarium, is annotated *Fucus amphibius*.

II. Lectotype: a pre-Linnaean illustration

EXAMPLE a. *Conferva imbricata* Huds. [*Halurus equisetifolius* (Lightf.) Kütz.]

The original description of *Conferva imbricata* first appears in the second edition of *Flora anglica* (Hudson, 1778:603), printed as followed:

> 44. CONFERVA filamentis geniculatis ramosissimis, ramis acutis, ramulis verticillatis imbricatis dichotomis. *imbricata.*
> Muscus marinus hirsutus, flagellis longioribus, rarius divisis, ruber. *Hist. Ox. III.* 650. *s.* 15. *t.* 9. *f.* 7.
> *Anglis,* imbricated Conferva.
> Habitat *in rupibus saxis et fucis marinis*. [perennial]. I–XII.

The original description of *C. imbricata* was obviously based on the previously-published illustration by Morison (1699: pl. 9, fig. 7), for which Hudson gave a partially erroneous citation, and on any material which Hudson might have had in his possession at the time of publication. Whether Hudson had material of his own is not obvious, the habitat notes being too vague and imprecise for any definite conclusion on this point.

The Morison illustration is somewhat stylized, but it would appear to be of the alga known currently as *Halurus equisetifolius* (Lightf.) Kütz., although the relevant material in the Morison Herbarium (OXF) consists of a herbarium sheet bearing two specimens, the larger of which is of that species, while the smaller is of the brown alga *Cladostephus spongiosus* (Huds.) C. Agardh. The discordant nature of the Morison material was first noted by Holmes (in Vines & Druce, 1914) and has been personally confirmed.

Conferva imbricata Huds. (1778) is antedated by *C. equisetifolia* Lightfoot (1777), the basionym of *Halurus equisetifolius*. In the appendix to the second edition of *Flora anglica*, Hudson (1778:663) cited the former as a synonym of *C. imbricata*, however. Four specimens of the taxon under discussion have been located at BM and all are specimens from the 'Hudson Sale', received through the Forster collection. The four specimens are named as *C. equisetifolia*, not *C. imbricata*, although the date of collection or acquisition by Hudson is not known.

The Morison illustration is selected here as the lectotype of *Conferva imbricata* Huds.

EXAMPLE b. *Fucus pinnatifidus* Huds. [*Laurencia pinnatifida* (Huds.) Lamouroux]

The original description of *Fucus pinnatifidus* by Hudson (1762:473) is printed as follows:

> 32. FUCUS frondibus planis ramosis, ramis dentato-pinnatifidis marginibus callosis. *pinnatifidus.*
> Fucus dealensis pedicularis rubræ folio. *Mus. pet.* 405. *R. Syn.* 48.
> Alga cervi cornu divisura. *B. hist. III.* 797.
> *Anglis,* jagged Fucus.
> Habitat *in saxis et rupibus marinis. Found about* Deal *by Mr.* Dandridge. *R. Syn. in littore* Devoniæ *frequens.*

This description was clearly based upon four elements:

1. the previous treatment by Petiver (1695–1703:39);
2. the previous treatment by Dillenius in Ray (1724:48);
3. the previous treatment by Bauhin (1651:797);
4. material collected in Devon as that county is not cited specifically in any of the preceding three elements.

The synonyms cited by Hudson are taken almost directly from those quoted previously by Dillenius in Ray (1724:48), whose treatment is printed as follows:

> * 37. Fucus Dealensis Pedicularis rubrifolio *Mus. Pet.* 405. Alga Cervi cornu divisura *J.B. III.* 797. Found about *Deal* by *Mr. Dandridge, Mr. Bonavert,* and *Mr. John Lufkin.*

This treatment by Ray was obviously based predominantly on the Petiver reference but with an additional citation of Bauhin (1651).

The Petiver specimen is in the Sloane Herbarium (vol. 150 folio 25) (BM-SL) and consists of two fragments with a printed extract '405. Fucus *Dealensis* Pedicularis rubræ folio. *My ingenious Friends Mr.* Dandride, *Mr.* Bonavert, *and Mr.* John Lufkin, Apothecary *at* Colchester, *have all observed this elegant* Fucus *about* Deal'. Associated with it are two hand-written labels, in Petiver's hand and Buddle's hand respectively. The specimen is of the alga known today as *Laurencia pinnatifida* (Huds.) Lamouroux.

The *Alga cervi cornu divisura* of Bauhin (1651) was not based upon an alga. Juel (1936:136) has shown that the specimen in the Bauhin Herbarium at Basel (BAS) labelled 'Alga cornu cervi divisura Bauh. Dedit Bauhinus ab Imperato acceptem' is a lichen of the genus *Ramalina*.

Two Hudson specimens are known to exist; one is a 'Hudson Sale' specimen received at BM through Forster and the other (in BM-K) is a specimen collected by Frankland at Scarborough. The former specimen bears no annotation indicating that it was collected in Devon, or that it was in Hudson's possession prior to the publication of the first edition of *Flora anglica*, so that neither appears to be directly relevant to the typification of *Fucus pinnatifidus* Huds.

The Petiver specimen is the most appropriate selection as the lectotype of *Fucus pinnatifidus* Huds., supporting both old (i.e. near-contemporary) and modern opinion as to the application of the epithet. Bauhin's polynomial, the only discordant element, can be discounted as Hudson did not see the specimen on which it was based.

EXAMPLE C. *Fucus plumosus* Huds. [*Ptilota plumosa* (Huds.) C. Agardh]

The original description of *Fucus plumosus* given by Hudson (1762:473) is printed as follows:

> 35. FUCUS caule teretiusculo compresso ramoso, ramis duplicato pinnatis coloratis. *plumosus.*
> Fucoides purpureum eleganter plumosum. *R. Syn.* 38. *t.* 2. *f.* 5.
> *Anglis,* Feathered Fucus.
> Habitat *in littoribus marinis passim.*

This description was based on two elements:

1. an illustration given by Dillenius in Ray (1724: pl. 2, fig. 5);
2. material in Hudson's possession, suggested by the general statement of occurrence rather than the single specific locality (Dover, Kent), cited by Ray.

Ray's illustration is somewhat stylized but is clearly of the alga known currently as *Plumaria elegans* (Bonnem.) Schmitz, not that known as *Ptilota plumosa* (Huds.) C. Agardh.

The Dillenius in Ray (1724:38) treatment is as follows:

> * 2. Fucoides purpureum eleganter plumosum. Muscus marinus eleganter plumosus, obscure purpurascens *Buddl. H. S. Vol. I. f. 29.* A *D. Rand* prope *Dover collectus*. Figuram vid. Tab. 2. fig. 5.

This shows that *Fucoides purpureum eleganter plumosum* was based on a specimen in the Buddle herbarium (BM-SL, vol. 114 folio 29) which is also of *Plumaria elegans*.

Although not relevant to the typification of the Dillenius in Ray entity, it is interesting to note that the material of *Fucoides purpureum* . . . in the *Synopsis* herbarium (OXF), collected at Llanfaethly (north Wales), is also of *P. elegans* (cf. Druce & Vines, 1907: 21).

Three specimens referred to *Fucus plumosus* Huds. which are said to have been in Hudson's possession are known to exist. These are as follows:

(*a*) a specimen from the Lambert herbarium, now in BM-K;

(*b*) a specimen from the Forster herbarium, at BM;

(*c*) a specimen from the Pulteney herbarium, said to be annotated in Hudson's hand, at BM.

All are of the alga known currently as *Ptilota plumosa*, although it is not possible to ascertain the date at which Hudson referred these specimens to his *Fucus plumosus*.

Thus, the Dillenius in Ray illustration and the Buddle specimen on which that was based are of one entity, whereas such Hudson material as has been located is of another. This discrepancy is curious as it is known that Hudson had access to the Sloane Herbarium, into which the Buddle herbarium has been incorporated in 1715. There appears to be no alternative to accepting the Ray illustration as lectotype of *Fucus plumosus* Huds. since the specimens said to have been identified by Hudson may not have been available to him in 1762.

All specimens subsequently attributed to *Fucus plumosus* Huds., are referable to a species different from the lectotype selected above. The reason appears to lie in the change between the two editions of *Flora anglica*. The first edition treatment has been quoted above; that of the second edition is printed as follows (p. 587):

47. FUCUS fronde cartilaginea compressa ramosa, ramis duplicato-pinnatis, fructificationibus pedunculatis globosis radiatis. *Fl. angl.* 473. *Gmel. fuc.* 152. *plumosus.*
Fucus frondibus cartilagineis lanceolatis bipinnatis plumosis, caule filiformi compresso ramoso. *Mant.* 134. *Syst. nat.* 718. *Fl. dan.* 350.
Fucoides purpureum eleganter plumosum. *R. syn.* 38. *t.* 2. *f.* 5.
Anglis, plumous Fucus.
Habitat *in rupibus et saxis submarinis.* [perennial] VII–X.

Although this is one of the few instances where Hudson's treatment of a species in the second edition refers back to the first edition (by his citation of 'Fl. Angl. 473.'), the descriptions in the two editions differ markedly. Hudson added in the second edition references to treatments of *Fucus plumosus* by Linnaeus (1767, 1774), Gmelin (1768) and Oeder (1767), the two latter being illustrated. Both illustrations (Gmelin, 1768: pl. 152 and Oeder, 1767: pl. 350) are of the alga to which the binomial *Ptilota plumosa* is currently applied rather than to *Plumaria elegans,* the alga of the lectotype. It would appear therefore that Hudson was influenced by the references and illustrations which he quoted in the treatment of *Fucus plumosus* in the second edition and his concept of the species changed completely. The specimens of *F. plumosus* which are said to have been in his possession represent material identified at a later date, after the change.

It is surprising that the identity of the alga described and illustrated by Dillenius in Ray and quoted by Hudson has not been questioned previously, particularly as the epithet *plumosus* is apparently derived from the Ray polynomial. The alga known currently as *Plumaria elegans,* to which the lectotype is referable, is plumose and usually purple-coloured, whereas the alga known today as *Ptilota plumosa* is not obviously plumose; it is bipinnate and carmine-red. Secondly, the alga known currently as *Ptilota plumosa* is of northern distribution in the British Isles, not occurring in an attached state south of Yorkshire on the east coast and Caernarvon on the west. Dover, the specific locality cited by Ray, is some 250 miles south of the southern limit of *Ptilota plumosa.*

The nomenclature of the genera *Plumaria* and *Ptilota* is already confused (cf. Silva, 1952) and the present discovery makes that situation worse. Full discussion and resolution of these problems are beyond the scope of the present paper, but a full morphological and nomenclatural study of the North Atlantic Ptiloteae is now approaching completion, as part of the preparatory work for *Seaweeds of the British Isles,* Volume 1, Part 3.

III. Lectotype (provisional): a Hudson specimen

EXAMPLE a. *Conferva elongata* Huds. [*Polysiphonia elongata* (Huds.) Sprengel]

The original description of *Conferva elongata* Hudson (1762:484) is printed as follows:

elongata. 25. CONFERVA filamentis geniculatis ramosissimis, ramulis longissimis distantibus acutis.
Conferva marina geniculata ramosissima lubrica, longis sparsisve ramulis. *R. Syn.* 61. *Dill. musc.* 35. *t.* 6. *f.* 38.
Anglis, Pointed Conferva.
Habitat *in littoribus marinis frequens.*

The description was based on three elements:

1. the previous treatment by Dillenius in Ray (1724:61);
2. the previous treatment and illustration by Dillenius (1742);
3. possibly material in his own possession, although the description and distribution are too imprecise for definite proof.

The treatment by Dillenius (1742:34) was clearly based directly on the earlier Ray (1724) account by Dillenius. The material now in the *Historia Muscorum* herbarium (OXF) preserved under the Dillenian name consists, as was shown by Batters (in Druce & Vines, 1907: 190), of four specimens. Three of these are referable to the genus *Ceramium,* while the fourth is of the alga known today as *Polysiphonia nigrescens*. The illustration given by Dillenius (1742: pl. 6, fig. 38) is too imprecise to allow specific identification, although it most likely refers to a species of *Ceramium*.

The previous treatment by Dillenius in Ray (1724:61) is printed as follows:

> * 23. Conferva marina geniculata ramosissima lubrica, longis sparsisve ramulis. Muscus marinus capillaris rubens geniculatus ramosissimus *Buddle Hort. Sicc.* Sent to him by *Mr. Stevens* from *Cornwal.* It is else common enough at *Cockbush, Sussex,* and about *Sheerness*.

The Ray description was based principally on material in the Buddle herbarium, with additional material from Kent and Sussex. There are now in BM-SL vol. 114 folio 30, two specimens labelled 'Muscus marinus capillaris rubens geniculatis ramosissimis Buddle N.D. sent by Mr Stevens from Cornwall'. These are of species of *Ceramium*; one specimen is dark red while the other is bleached. Dillenius (1742) comments on this alga—'color rubicundiis, interdum arenaceiis'. The specimens currently in the *Synopsis* herbarium (OXF) consist of a mass of material largely collected by Brewer in north Wales, with no trace of any collections from Cornwall, Kent or Sussex. The indications are therefore that the original treatment of *Conferva elongata* Huds. referred to material of species of both *Ceramium* and *Polysiphonia*.

The treatment in the second edition of Hudson (1778:599) is very different, however:

> 27. CONFERVA filamentis geniculatis ramosis, ramis dichotomis longis setaceis, articulis brevissimis. *elongata.*
> *Anglis,* pointed Conferva.
> Habitat *in saxis et rupibus submarinis, in* Devonia, Cornubia, Sussexia, *et in insula* Mona, *passim.* [annual]. IV–X.
> Desc. Fila *dodrantalia et pedalia, crassitie fili emporetici tenuioris, articulata, lævia, fusco-purpurea, basi ramosa*; Rami *dichotomi, longissimi, setacei*; *articulis brevissimis*.

The two diagnoses differ, two localities were added (Devon, Anglesey), one of the original localities (Kent) was deleted, and a considerable amount of descriptive material was included in the second treatment. Most importantly, the Ray and Dillenian synonyms of the first treatment are transferred to the synonymy of *Conferva rubra,* the basionym of *Ceramium rubrum.* Furthermore, contemporary views on *Conferva elongata* Huds., such as Dillwyn (1803) and Smith & Sowerby (1790–1814) accord with current application of the epithet to a species of *Polysiphonia.* There is a specimen in BM, received through the Forster herbarium from the 'Hudson Sale' and labelled '*Conferva elongata*', which is correctly identified as *Polysiphonia elongata* (Huds.) Sprengel (as currently understood) and filed in a type folder. The sheet also bears a *determinavit* label '*Polysiphonia elongata* (Huds.) Grev. ex Harv. in Hook = *Conferva elongata* Hudson probably in sense of Ed. II 1778 p. 599 . . . A. R. A. Taylor 1.IX.64', in A. R. A. Taylor's hand.

Although the initial treatment of *Conferva elongata* Huds. was based on material which was heterogeneous, the treatment in the second edition was not; near-contemporary and current usage is in complete agreement as to the application of the epithet, supported by a specimen of the entity originating from Hudson. It can be postulated that Hudson eventually appreciated that his original description was based on several discordant elements and that the 'improved' text of the later treatment in the second edition represents a careful selection from that original miscellany, a procedure which is common nomenclatural practice nowadays. The specimen in BM has therefore been selected as provisional lectotype of *Conferva elongata* Huds.

EXAMPLE b. *Fucus plicatus* Huds. [*Ahnfeltia plicata* (Huds.) Fr.]

The original description of *Fucus plicatus* by Hudson (1762:470) is printed as follows:

plicatus. 19. FUCUS capillaris uniformis ramosissimus implicatus
subdiaphanus.
Fucus trichoides nostras aurei coloris, ramulorum apicibus furcatis. *Pluk. ph. t.* 184. *f.* 2. *R. Syn.*
45.
Fucus coralloides erectus. *R. Syn.* 51.
Anglis, Matted Fucus.
Habitat *in littoribus marinis.*

This was based on:

1. an illustration by Plukenet (1696: pl. 184, fig. 2);
2. the previous treatment by Ray (1724:45).

The general statement of localities provided by Hudson is too imprecise to be certain that he had his own specimens at the time of publication of the original description, but his extended description suggests that he did.

The reference to the Plukenet illustration was taken from the previous treatment by Ray (1724:45), which is as follows:

> 26. Fucus trichoides nostras aurei coloris, ramulorum apicibus furcatis *Pluk. Alm.* 160. *T.* 184. *f.*2. Alga exigua dichotomos arenacei coloris *Syn. II.* 4. 10. Fucus ceranoides ramosus tenuissime divisus *Dood. Syn. II. App.* 329. Palmaris est, corneus tenax, albus, per siccitatem rigidus, ubique ejusdem fere crassitudinis, quæ filum parvum superat. In littore *Essexiano, Sussexiano* & alibi.

Both Dillenius in Ray (1724) and Hudson (1762) refer to an illustration by Plukenet (1696: pl. 184, fig. 2). This illustration is poor and it is not possible to state categorically that it represents the alga known currently as *Ahnfeltia plicata.* Plukenet's herbarium has been incorporated into BM-SL and the reverse of Folio 80 of Volume 84 bears a specimen labelled 'Alga marina trichodes lutea. S. Trichoman. ceranoides marin. [deleted] aurea & ramosa, ramulos apicis furcatis' in Plukenet's hand. This specimen could possibly have formed the basis for the Plukenet illustration which it resembles in shape, proportions and branching pattern, and it is also of the alga known currently as *Ahnfeltia plicata.* A second specimen of *A. plicata* bearing a different annotation is mounted on folio 81. The specimens in this volume of the Sloane Herbarium are arranged in alphabetical order, and the two specimens in question occur among species of *Fucus,* the genus to which Plukenet referred his entity in his publication (Plukenet, 1696). Although it is known that Hudson had access to the Sloane Herbarium, there is no annotation or other indication that he actually examined these specimens. In other cases where Hudson had examined material in the Sloane Herbarium, as with *Fucus plumosus* (Example IIc) and *Fucus pinnatifidus* (Example IIb), he made reference to the actual specimen, but he did not do so in this case. As noted above, Hudson may have had material of his own to hand when he drew up the original description of *Fucus plicatus.* A specimen labelled *Fucus plicatus* at BM, received from the Forster herbarium and annotated as having been obtained from the 'Hudson Sale', is of the alga known today as *Ahnfeltia plicata.* In view of the uncertainties surrounding the Ray and Plukenet synonyms, this specimen has been designated as the provisional lectotype of *Fucus plicatus* (see Dixon & Irvine, 1977*a*).

The infraspectific entity in the original treatment of *Fucus plicatus* is based directly on the *Fucus coralloides erectus* of Dillenius in Ray (1724) which is a repetition of an entry in an earlier Ray (1704) publication. As Hudson gave no locality presumably he had no material of his own. The material in the *Synopsis* herbarium (OXF) referred to this entity was tentatively identified by Holmes (in Druce & Vines, 1907:26) as the freshwater red alga *Lemanea fluviatilis* (L.) C. Agardh. It consists only of a few scraps, and is difficult to confirm from personal examination, but Holmes's identification was probably correct. Thus, the infraspecific entity described by Hudson has no connection with *Fucus plicatus* Huds.

IV. Lectotype: a Hudson description

EXAMPLE a. *Conferva fucoides* Huds. [*Polysiphonia nigrescens* (Huds.) Grev.]

The original description of *C. fucoides* (Hudson, 1762:485) is printed as follows:

> 31. CONFERVA filamentis geniculatis ramosissimis ramulis multifidis fasciculatisque. *fucoides.*
> *Anglis,* Branched Conferva.
> Habitat *in littore* Eboracensi.

This description was obviously based on Hudson's own material. The treatment in the second edition (Hudson, 1778:603) differs in various ways, and is printed so:

> 42. CONFERVA filamentis geniculatis ramosissimis ramulis multifidis, inferioribus fasciculatis fructiferis. *fucoides.*
> *Anglis,* fucus Conferva.
> Habitat *in rupibus, saxis et fucis marinis passim.* [perennial]. I–XII.
> Desc. Fila *pedalia, geniculata, lævia atro-rubescentia, ramosissima,* Rami *alterni*; *ramuli multifidi, subdichotomi, inferiores fasciculati, fructiferi.* Fructificationes *terminales, radiatæ, parvæ.*

There are no extant specimens of Hudson's referred to this entity although several contemporary specimens have been located which are relevant, the most important of these being specimens originating from Frankland. One of these is in the collection which was at LINN (Dixon, 1959*a*) and is now at BM; this is said to be illustrative of Hudson's application of the name. The other Frankland specimen occurs in the Lightfoot herbarium (now at BM) and is annotated 'named repeatedly by Hudson *C. fucoides*.' Both Frankland specimens are of the alga known currently as *Polysiphonia nigrescens*. Dillwyn (1802–09 fasc. 10: pl. 75), in his treatment of *Conferva fucoides,* comments 'The [taxonomic] difficulty in the present species has been removed by the kindness of my friends the Rev. Hugh Davies and Archibald Menzies, who, from among some authentic specimens which they fortunately possess, have obligingly spared me two pieces marked "C. fucoides" exactly corresponding with the plant here figured . . .'. Unfortunately, no trace of these can be found at present among Dillwyn's herbarium materials, which are now much scattered (Dixon, 1966), neither can any relevant Hudson material once belonging to either Menzies or Davies be traced. There are, however, several specimens which were once in Davies's possession, and referred by him to *C. fucoides*, in BM-K; these are all of the alga known currently as *Polysiphonia nigrescens*. Later Dillwyn added an Introduction and Synopsis to the fascicles of plates of *British Confervae* (1802–09). In the Synopsis (p. 81) he was still not convinced that *C. fucoides* was distinct from *C. nigrescens*. Although no authentic herbarium material can be located at the present time, near-contemporary opinion was unanimous in referring the entity to the alga known today as *Polysiphonia nigrescens,* and provides a basis for accepting *Conferva fucoides,* lectotypified by the original description, as a synonym of *Polysiphonia nigrescens*.

EXAMPLE b. *Conferva nigra* Huds. [*Polysiphonia nigra* (Huds.) Batters]

The original description (Hudson, 1762:481) is brief, printed as follows:

> 12. CONFERVA filamentis æqualibus ramosis, ramis faciculatis brevissimis. *nigra.*
> *Anglis,* black Conferva.
> Habitat *in littore* Eboracensi *copiose*.

The later treatment (Hudson, 1778:595) is more detailed, but no synonyms or specimens are added:

15. CONFERVA filamentis æqualibus ramosis longissimis, ramis alternis multifidis brevissimus. *Fl. angl.* 481. *nigra.*
Anglis, black Conferva.
Habitat *in littore* Eboracensi *passim.* [annual]. V–X.
Desc. Fila *quinque pollicaria, æqualia, rigidiuscula, nigra, ramosa, ramis alternis brevissimis multifidis, fasciculatis.*

This indicates that the species was one of those described by Hudson on the basis of his own material. Contemporary workers referred the entity to the alga to which the epithet is now applied. For example, Dillwyn (1802–09 fasc. 10: pl. 70) had described *C. atro-rubescens* but stated later (Dillwyn 1802–09 fasc. 15: pl. 101) that 'Authentic specimens with which I have been favored by Sir Thomas Frankland and the Rev. Hugh Davies, prove that Hudson's *Conferva nigra*, respecting which I had previously been accustomed to yield to the generally received opinion of its being the same as *Fucus fruticulosus,* is in reality the *C. atro rubescens* of this work'. There is no trace at the present time of any such relevant material in BM, BM-K, or in the Lightfoot herbarium at BM-K. The volume of Dillwyn specimens at NMW contains several specimens on p. 202, with a label in which *atro-rubescens* is crossed through and replaced by *nigra.* One curious piece of information is provided by Batters (1902:81) in making the combination *Polysiphonia nigra* (Huds.) Batters. Here he stated that his transfer of *Conferva nigra* is based 'e spec. auth. in Herb. Brit. Mus.' but there is no 'authentic specimen' of *Polysiphonia nigra* at the present time in BM.

Since there is no evidence suggesting any misapplication of the epithet, it can be typified by the description given by Hudson (1762:481).

V. Species inquirenda

EXAMPLE a. *Conferva fulva* Huds. [unassigned]

The original description of *Conferva fulva* (Hudson, 1762:484) is extremely brief:

fulva. 26. CONFERVA filamentis geniculatis ramosis, ramis ramulisque brevissimis alternis.
Anglis, short Conferva.
Habitat *in littore* Eboracensi.

The treatment in the second edition (Hudson, 1778:602) is slightly changed and expanded. It is printed as follows:

fulva. 39. CONFERVA filamentis geniculatis ramosis, ramis ramulisque brevissimis fulvis.
Anglis, tawny Conferva.
Habitat *in saxis et fucis marinis, in littore* Eboracensi. [annual]. V–IX.

No synonyms are cited in either treatment, so that the species must have been described entirely from Hudson's own material. The entity has been a matter of conjecture for many years. Dillwyn (1802–09 fasc. 2: pl. 18) in his original description of *Conferva repens* (= *Spermothamnion repens*) stated: 'May not the present be Hudson's C. fulva, the description of which, in the Flora Anglica, is unfortunately so short, that unless any authentic specimen of it exists, which I believe there does not, it will always be impossible to tell what he meant by that name'. Later Dillwyn (1802–09 Introduction:34), in an analysis of species of *Conferva* treated by Hudson, commented with respect to *C. fulva* 'I suspect that *C. repens*, T. 18, is the plant here designed, but proof is wanting'.

Thus, *Conferva fulva* Huds., is an entity of unknown assignment at the present time and one about which near-contemporary authors were uncertain. In both editions of *Flora anglica* the treatments are very brief and equally referable to many red or brown algae. There is thus good reason for accepting that *C. fulva* is a species which cannot yet be typified.

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Seaweeds of the Faroes

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NATURAL HISTORY
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Seaweeds of the Faroes
1: The flora

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Synopsis

A brief description of the Faroes is followed by an account of earlier phycological investigations and the reasons for carrying out a general survey of the marine algae at the present time. A list of the known seaweed flora is given, including the records of previous investigators, with brief habitat and distribution notes, and records of occurrence in the Orkneys, the Shetland Isles, and Iceland.

The flora is shown to be similar to that of the Shetland Isles, though much poorer in species, but with a few subarctic species in the north which have not so far been found in the British Isles. It shows remarkably few changes from that described by Børgesen and his colleagues around the end of the 19th century. Some species not recorded by us, e.g. *Porphyra linearis*, may have been present earlier in the season. If dubious records are excluded, 9 Cyanophyta, 95 Rhodophyta, 74 Phaeophyta, 44 Chlorophyta, and 1 marine *Vaucheria,* 223 spp. in all are recorded, whereas 301 spp. have been found in the neighbouring Shetland Isles.

1. Introduction

The Faroes (Færøerne; Faeroes; Føroyar) are a group of 18 islands and innumerable rocks, stacks and skerries, with an area of 1325 sq. km (Fig. 1). The islands lie mainly in the Gulf Stream, but a cold north-westerly current impinges on the northernmost islands of the group (Fig. 2). They lie about halfway between the Shetland Isles and Iceland, and are under the protection of Denmark, but have been self-governing since 1948.

The population is about 50 000, mostly forming scattered communities fringing the deeply indented coastline. The capital, Tórshavn, is a thriving port in the centre of the group, and the other main population centre is the fishing village of Klaksvík in the northern group of islands. To the west and the north the shores tend to be precipitous with only a minimal littoral, and access from the land is not practicable over large stretches. The islands are deeply penetrated by narrow fjords and separated by equally narrow sounds. The tidal range is small, but the littoral is effectively greatly extended by wave surge and spray. The climate is mild, with an annual rainfall

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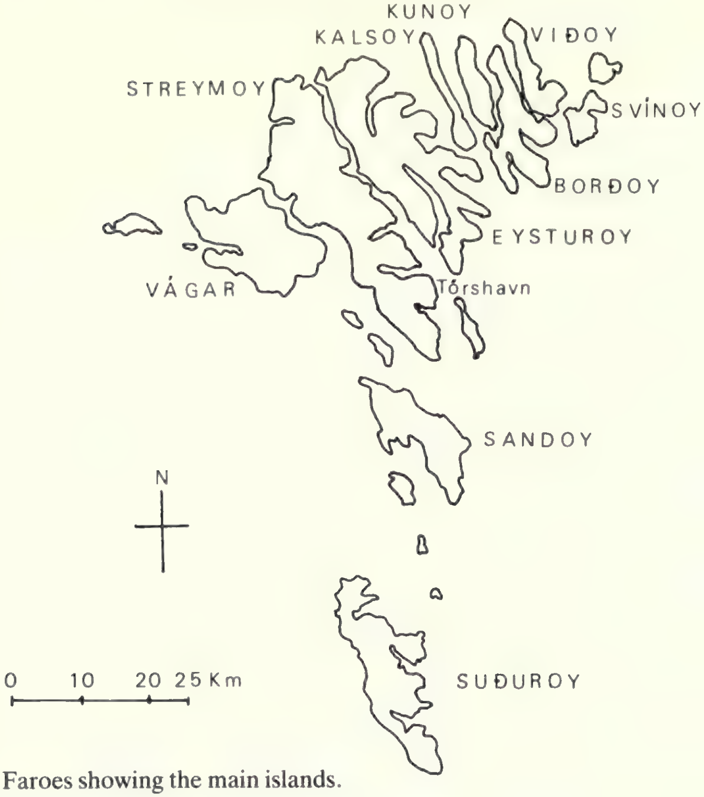

Fig. 1 Map of the Faroes showing the main islands.

of about 1600 mm; conditions are generally cloudy and fogs are frequent in the summer months, while gales may occur at any season.

The seaweeds of the Faroes have been investigated at various times, notably by H. C. Lyngbye (1819), E. Rostrup (1870) and H. G. Simmons (1897), and a definitive survey was carried out by F. Børgesen and various colleagues and published in a series of papers from 1895 to 1905. Børgesen was able to make several visits to the islands, and with the co-operation of the Danish Marine Department was able to spend long periods on a fisheries protection vessel from which he was able to visit many of the otherwise inaccessible shores and to have dredging facilities. Although he only visited the islands in spring and summer, H. Jønsson provided him with an extensive collection made in autumn and early winter. The contributions of other workers are listed in detail in the introduction to Børgesen's account of the marine algae (1902).

Since the papers of Børgesen, surprisingly little has been published concerning the marine algae of the Faroes, although their flora is of obvious interest to phycologists working in the North Atlantic area. B. Rex carried out some studies of vegetation profiles on several shores in 1970. His most important find was that *Dilsea carnosa* is common in the subtidal. It had been recorded earlier by P. A. Holm (1855), but as later investigators, including Børgesen, had not found it, this record has been discarded by Børgesen. In 1975 G. Holt compared the seaweed floras (including blue-green algae and diatoms) of eight widely differing sites, using a large number of different stations at each site. His work, however, did not produce many additions to the known seaweed flora.

2. Methodology

It was hoped that an intensive study of the intertidal and subtidal vegetation of the Faroes, using boats and modern diving equipment, would show the Faroese algal flora to be much richer in

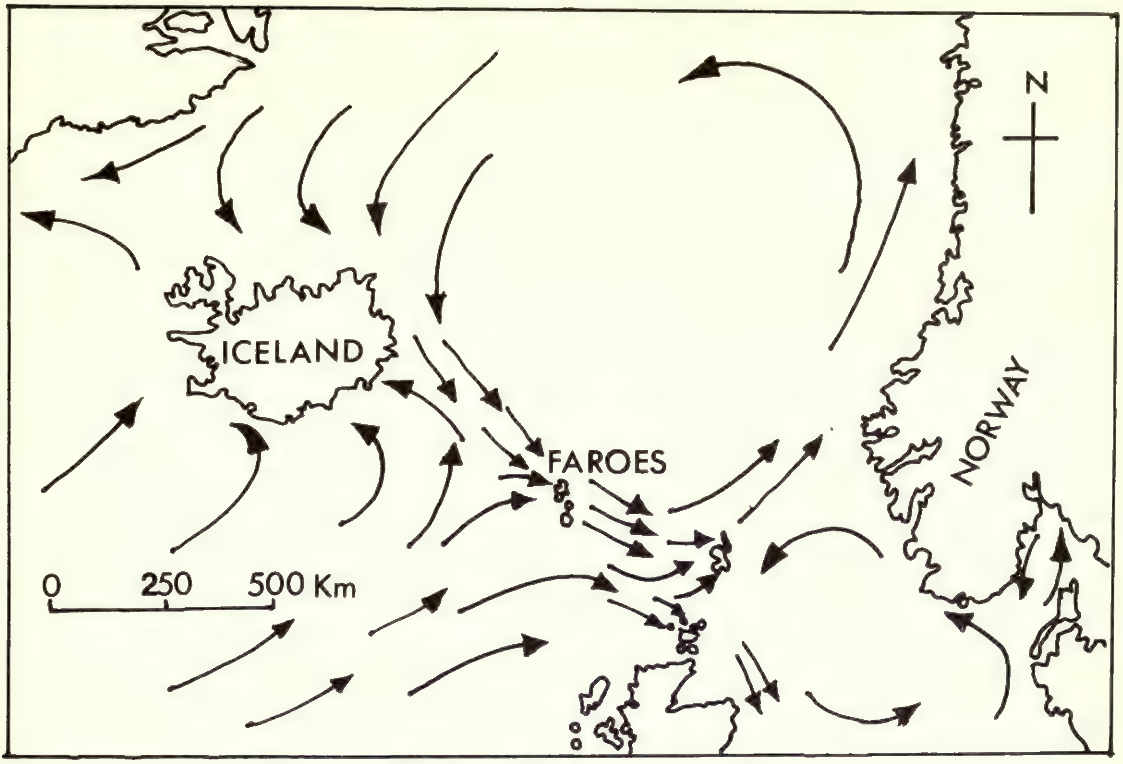

Fig. 2 Map showing position of the Faroes in relation to main ocean currents and neighbouring land masses (after Ryder in Børgesen 1905: 813).

species than the findings of the earlier workers had indicated; this had been the case in a similar investigation carried out in the Shetland Isles (Irvine, 1974). Accordingly, a rather flexible expedition was arranged for 1980, based on two laboratories in Tórshavn kindly lent by the Academia Faeroensis and formed of a number of semi-independent groups and individual scientists from various countries who stayed for limited periods. Although they largely pursued their own special interests, their contributions to this species list were of considerable importance.

The main group was based on Tórshavn for two weeks in early July 1980, then a week at Viðareiði in the northern island of Viðoy, followed by a week in Tórshavn. Most of the major islands, apart from Suðuroy, were examined both intertidally and subtidally (using inflatables and scuba equipment), and particular attention was given to Skálafjørður, a large fjord in Eysturoy, not unlike Sullom Voe in the Shetland Isles in some respects. Extensive collections were made, and the species list which follows is an amalgam of earlier records and of the observations and collections of all the members of this expedition.

3. Species list

The nomenclature chiefly follows Parke & Dixon (1976) for taxa which also occur in the British Isles, although many abbreviations of authors' names are revised to accord with editorial requirements.

Abbreviations:
(!) Recorded on the 1980 expedition.
* New to the Faroes.
O. Recorded from the Orkneys.
S. Recorded from the Shetland Isles (Irvine, 1980).
I. Recorded from Iceland (Caram & Jónsson, 1972).
[ ] Name used by Børgesen (1902). Note that Børgesen's place names have been changed to Faroese.

CYANOPHYTA

Calothrix crustacea Thuret ex Bornet & Flah. [*C. aeruginea, C. scopulorum, Rivularia atra]*
Near high tide level. Widely distributed. (!) O. S. I.

Entophysalis conferta (Kütz.) Drouet & Daily [*Dermocarpa farlowi, D. violacea, Pleurocapsa amethystea*]
Epiphytic on various intertidal algae, notably *Polysiphonia lanosa.* Common, widely distributed. (!) O. S. I.

E. deusta (Menegh.) Drouet & Daily [*Hyella caespitosa, H. endophytica*]
In shells of molluscs, subtidally to 40 m. Found on Streymoy by Børgesen. O. S. I.

Microcoleus lyngbyaceus (Kütz.) P. Crouan & H. Crouan ex Gomont
Listed by Holt from Saksun under the names *Hydrocoleum glutinosum, Lyngbya semiplena, Merismopedia elegans, and Oscillatoria tenuis.* O. S.

M. vaginatus (Vaucher) Gomont ex Gomont [*Phormidium autumnale*]
Near high tide level, on wet rocks and in pools. Found by Børgesen on Kalsoy: Húsar, and on Streymoy: Tinganes. I.

Oscillatoria lutea Agardh ex Gomont [*Lyngbya luteà*]
Intertidally on somewhat exposed shores. Recorded by Børgesen from Viðoy: Viðvík, and Streymoy: Tórshavn. O.

Schizothrix calcicola (Agardh) Gomont
Listed by Holt from Tórshavn (as *Phormidium fragile)*. O. S. I.

S. tenerrima (Gomont) Drouet [*Microcoleus tenerrimus*]
Found once by H. Jønsson at Hvannasund.

Spirulina subsalsa Oersted ex Gomont
In rock pools on moderately exposed shores. Recorded by Børgesen from near Tórshavn and by Holt (as *S. subtilissima*) from Saksun. O. S. I.

RHODOPHYTA

Actinococcus subcutaneus
The sporophyte phase of *Phyllophora truncata* (q.v.) parasitic on the gametophyte.

Ahnfeltia plicata (Huds.) Fr. [including *Sterrocolax decipiens*]
Lower intertidal and shallow subtidal, in sheltered fjords and bays. Locally common. (!) O. S. I.

Antithamnion boreale (Gobi) Kjellman [*A. plumula* var. *boreale*]
Subtidally to 50 m, mainly on sheltered shores. O. I.

A. floccosum (Müll.) Kleen
Intertidal and shallow subtidal, mainly on sheltered shores. Occasional, widely distributed. (!) O. S. I.

A. plumula (Ellis) Thuret

Subtidal on rocks, shells, and epiphytic, exposed and sheltered shores. Widely but sparingly distributed. (!) O. S. (I?).

Audouinella alariae (Jónsson) Woelk. [*Chantransia Alariae*]

Shallow subtidal on *Alaria* fronds, especially on exposed shores. Widely distributed and generally abundant, although Børgesen recorded it only from Streymoy: near Tórshavn. (!) O. S.

A. daviesii (Dillwyn) Woelk. [*Chantransia Daviesii*]

Subtidal on various algae. Widely distributed. (!) O. S.

A. efflorescens (J. Agardh) Papenf. [*Chantransia efflorescens*]

On sheltered coasts, subtidally, epiphytic on various algae. Eysturoy.

A. membranacea (Magnus) Papenf. [*Rhodochorton membranaceum*]

Intertidally and subtidally, to 40 m, sheltered and exposed coasts, on Bryozoans, often with *A. spetsbergensis*. Widely distributed, probably common but overlooked. I.

A. purpurea (Lightf.) Woelk. [*Rhodochorton Rothii*]

On rocks in caves, fissures, and waterfalls, from the upper spray zone downwards intertidally, and epiphytic on stipes of *Laminaria hyperborea* subtidally to about 20 m, commonly on exposed shores. Abundant and widely distributed. (!) O. S. I.

A. secundata (Lyngbye) P. Dixon [*Chantransia secundata*]

Epiphytic on various algae, intertidal on exposed and sheltered shores. Widely distributed, common. (!) O. S. I.

A. seiriolana (Harvey-Gibson) P. Dixon [*Rhodochorton seiriolanum*]

Recorded by Børgesen as epiphytic on *Ceramium shuttleworthianum* on an exposed coast, near high-water mark. Streymoy: Velbastaður. Otherwise known only from the type locality [Anglesey (Wales): Puffin Island].

A. spetsbergensis (Kjellman) Woelk. [*Rhodochorton penicilliforme*]

Intertidally and subtidally to 40 m, on Bryozoans. Widely distributed but sparsely recorded; probably overlooked. (!) S. I.

A. virgatula (Harvey) P. Dixon [*Chantransia virgatula*. Probably Lyngbye's *Callithamnion lanuginosum* belongs here, fide Børgesen, though Rostrup identifies it with *A. daviesii*.]

Epiphytic on various algae intertidally and subtidally, on sheltered and exposed shores. Common and widely distributed. (!) O. S. I.

Bangia atropurpurea (Roth) Agardh [*B. fuscopurpurea*]

On rocks intertidally from upper spray zone downwards, especially on exposed shores, often associated with *Urospora* and *Ulothrix* spp. Scattered filaments occurred intermingled with larger algae. Common and widely distributed. See *Conchocelis*. (!) O. S. I.

Bonnemaisonia hamifera Hariot

See *Trailliella*.

***Brongniartella byssoides** (Gooden. & Woodw.) Schmitz

On rocks subtidally on moderately exposed shores. Rare, widely distributed. (!) O. S.

Callithamnion corymbosum (Sm.) Lyngbye (as var. *amphicarpa*)

Epiphytic subtidally at about 16 m. Eysturoy: near Oyri, a few fronds only. O. S.

***C. decompositum** J. Agardh

Epiphytic subtidally. Occasional. (!) S.

[**C. granulatum** (Ducluz.) Agardh

Recorded by Børgesen, but almost certainly in error. All Faroese specimens distributed in herbaria under this name appear to be referable to *C. hookeri* (Dixon & Price, 1981) and no specimens of *C. granulatum* could be found at any of the sites listed for it by Børgesen. O. S.]

C. hookeri (Dillwyn) Gray [*C. polyspermum, C. scopulorum*]
On rocks and epiphytic; in caves, fissures, and on open rock faces at about midtide level on exposed coasts. Common and widely distributed. (!) O. S. I.

C. sepositum (Gunnerus) P. Dixon & J. Price [*C. arbuscula*]
On rocks, barnacles, and *Mytilus* at midtide level on exposed coasts, especially on steeply sloping faces. Abundant, widely distributed. (!) O. S. I.

Callocolax neglectus Schmitz ex Batters
Parasitic on *Callophyllis laciniata* subtidally to 50 m. Generally distributed with the host and often common, but not observed intertidally. (!) O. S. I.

Callophyllis cristata (Agardh) Kütz. [*Euthora cristata*]
Epiphytic on haptera of *Laminaria hyperborea,* more rarely on rocks and shells, lower intertidal (rarely) and subtidal to 50 m, exposed to moderately sheltered coasts. Very varied in growth form, intertidal plants tending to be much branched and bushy. Widely distributed, common. (!) O. S. I.

C. laciniata (Huds.) Kütz.
On stones and shells and epiphytic, especially on the lower stipe and haptera of *Laminaria hyperborea,* in shady pools and subtidally to 50 m, in exposed to moderately sheltered localities. Common and widespread. (!) O. S.

Ceramium diaphanum (Lightf.) Roth
Intertidal and shallow subtidal, a few scattered fronds probably referable to this species. Recorded by Lyngbye (1819:119, pl. 37) from Tórshavn and Eiði, but these records dismissed by Børgesen as referring to *C. rubrum*. (!) O. S.

C. rubrum (Huds.) Agardh
Intertidal and subtidal, on rocks and epiphytic, on exposed to sheltered coasts. Widespread and abundant. Very variable in size and growth form. (!) O. S. I.

[**C. secundatum** J. Agardh
Recorded by Lyngbye (1819) from between Tórshavn and Hoyvik. Record dismissed by Børgesen as referring to a form of *C. rubrum*].

C. shuttleworthianum (Kütz.) Rabenh. [*C. acanthonotum*]
On rocks, barnacles, and *Mytilus*, in spongy tufts about midtide on exposed shores. Abundant, widely distributed. (!) O. S. I.

C. strictum Harvey
Recorded by Holt from Sandoy. S.

Chondrus crispus Stackh.
On rocks, midtide to shallow subtidal, exposed to sheltered shores, and in rock pools, often in dense stands. Neither Lyngbye nor Børgesen considered it common, but it is generally distributed and at least locally abundant. (!) O. S. I.

Choreocolax polysiphoniae Reinsch
Parasitic on *Polysiphonia lanosa.* Recorded only sparsely, but probably occurring generally where the host is present. First recorded by Børgesen (1905: 773). (!) O. S.

Clathromorphum circumscriptum (Strömf.) Foslie
Found once by Børgesen on Streymoy: in Sundini between Hósvík and Hvalvík. Later placed by Foslie in *Phymatolithon compactum* (Børgesen 1905: 773) but probably belongs to *Clathromorphum*. I.

Conchocelis (phase in the life history of spp. of *Bangia* and *Porphyra*)
Subtidal to 50 m, sheltered and exposed shores, and in shells. Common, widely distributed. (!) O. S. I.

Corallina officinalis L.
On rocks intertidally, in pools, and in shallow subtidal situations, on exposed to fairly sheltered shores, often in dense patches. Common, widely distributed. (!) O. S. I.

Cruoria pellita (Lyngbye) Fr.
Encrusting rocks, shells, and stones intertidally and subtidally, and epiphytic on the stipes and holdfasts of *Laminaria hyperborea* on both exposed and sheltered shores. Common and widely distributed. (!) O. S. I.

Cryptopleura ramosa (Huds.) Kylin ex Newton [*Nitophyllum laceratum*]
On rocks and amongst *Corallina* subtidally, as small prostrate specimens. Widely dispersed but not common. (!) O. S.

Cystoclonium purpureum (Huds.) Batters [*C. purpurascens*]
On rocks and stones in shallow subtidal, mainly on sheltered coasts. Lyngbye considered it rare, and Børgesen remarks 'This species does not appear to be widely distributed along the shores of the Faeroes'. However, we found it frequently, especially just below low water on sheltered shores. (!) O. S. I.

Delesseria sanguinea (Huds.) Lamouroux
On rocks, lower intertidal (in pools, caves, and deep crevices) and subtidally to 50 m, on exposed to sheltered shores. Common and widespread. (!) O. S. I.

Dermatolithon corallinae (P. Crouan & H. Crouan) Foslie
Epiphytic on *Corallina.* Common and widespread with its host. (!) S. I.

D. crouanii (Foslie) Lemoine [*Lithophyllum Crouani*]
Epiphytic on stipes and holdfasts of *Laminaria hyperborea,* associated with *D. pustulatum.* Eysturoy: Gjógv. Suðuroy: Lobra. I.

D. hapalidioides (P. Crouan & H. Crouan) Foslie
Noted by Ostenfeld on a *Patella* shell in Suðuroy: Hvannhagi. O.

D. pustulatum (Lamouroux) Foslie [*D. macrocarpum*]
Epiphytic on various algae (notably *Furcellaria, Gigartina,* and *Laminaria hyperborea*), intertidally and subtidally, exposed to sheltered shores. Abundant and widespread. (!) O. S. I.

Devaleraea ramentacea (L.) Guiry [*Halosaccion ramentaceum*]
On loose stones about low water mark and immediately below, on very sheltered shores; locally abundant in a few northern fjords over a limited area. Borðoy: Haraldssund (!) and near Klaksvík. Viðoy: Hvannasund (!). Streymoy: Vestmanna. It has also been recorded by Jønsson from Svínoy: near the Havn, on a fairly exposed shore on rocks near low water, but a close search of this very atypical site failed to reveal any specimens. There were, however, some stands of *Dumontia* with a growth form very similar to that of *Devaleraea*, and it seems likely that the original record was a misidentification. (!) I.

Dilsea carnosa (Schmidel) Kuntze
Recorded by Holm (1855) but not found by later investigators, and the record therefore dismissed by both Rostrup (1870) and Børgesen (1903). Nevertheless, it was found by both Rex (1970) and Holt (1975), and we found it to be abundant and generally distributed, growing on rocks in intertidal pools, and subtidally to *relatively shallow* depths. Discoloured specimens were widespread and prominent in the drift, and living specimens were large and healthy. Had it occurred like this in earlier times it could scarcely have been missed or confused with other species. It seems probable, therefore, that *Dilsea* has only entered the Faroes during this century, some time before 1970. (!) O. S. I.

Dumontia contorta (S. Gmelin) Rupr. [*D. filiformis*]
On rocks and stones, intertidally and in the shallow subtidal, on exposed and sheltered shores. Abundant, widely distributed. (!) O. S. I.

*__Erythrotrichia boryana__ (Mont.) Berthold
Eysturoy: Skálafjørður, Skálabotnur. (!) O.

*__E. carnea__ (Dillwyn) J. Agardh [*E. ceramicola*]
Intertidally and in the shallow subtidal as isolated filaments interwoven with other algae, such as *Ceramium shuttleworthianum* and *Corallina,* mainly on sheltered shores. Probably widely distributed but never abundant; easily overlooked. (!) O. S.

Fimbrifolium dichotomum (Lepechin) G. Hansen [*Rhodophyllis dichotoma*]
On stones and shells, and especially on stipes and haptera of *Laminaria hyperborea,* subtidally to about 50 m, on exposed to moderately sheltered shores in the northern islands. (!) I. [Fig. 3]

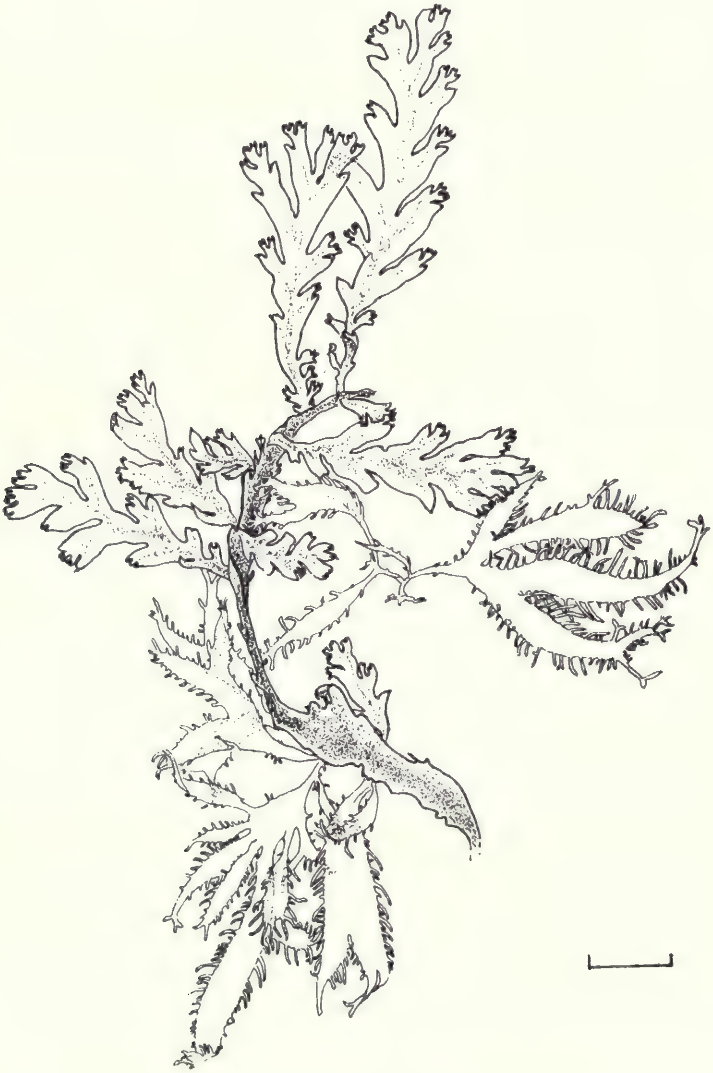

Fig. 3 Two specimens of *Fimbrifolium dichotomum* (Lepechin) G. Hansen growing with *Delesseria sanguinea* on *Odonthalia dentata*. The scale shows 1 cm. [This species has not so far been recorded from the British Isles, but should be looked for in north-east Scotland.]

Furcellaria lumbricalis (Huds.) Lamouroux [*F. fastigiatus*]
On rocks, lower intertidal (in pools) and subtidally to 20 m, on moderately exposed to sheltered shores, in dense but scattered patches. Frequent and widely distributed. (!) O. S. I.

Gigartina stellata (Stackh.) Batters [*G. mamillosa*]
On rocks, intertidal and immediate subtidal, on exposed coasts, often forming zones or large patches near low water on very exposed rock faces. Abundant and widely distributed. (!) O. S. I.

Goniotrichum alsidii (Zanard.) M. Howe
Recorded by Holt from Tórshavn as *G. elegans*. Not recorded from Orkney, Shetland or Iceland.

Griffithsia corallinoides (L.) Batters [*Conferva (Griffithsia) corallina*]
Reported by Landt (1800: 233) as occurring in the Faroes, but not found since. Possibly an error, but in Shetland it occurs on moderately sheltered coasts subtidally to 20 m. O. S.

G. flosculosa (Ellis) Batters [*G. setacea*]
On rocks, subtidally to 20 m, apparently very rare. Found by Børgesen as a single small specimen (Suðuroy: Trongisvagsfjørður) and during the present expedition by P. A. Åsen as a single small tuft. (!) O. S.

Harveyella mirabilis (Reinsch) Reinke
Parasitic on *Rhodomela confervoides*. Apparently rare. Kunoy (Jønsson). Suðuroy: Trongisvágur (Børgesen). A single specimen found by us. (!) I.

Hildenbrandia rubra (Sommerf.) Menegh. [*H. rosea*]
Intertidally and to the top of the spray zone, on open rocks and stones and in pools, on sheltered and exposed shores. Abundant and widespread. (!) O. S. I.

Laurencia pinnatifida (Huds.) Lamouroux
Intertidally on rocks and large stones on exposed and sheltered coasts, rare. Streymoy: between Tórshavn and Hoyvik (Rostrup). Suðuroy: Tvøroyri and Øravík (Ostenfeld). Searched for carefully, including the Streymoy site, but not found on the present expedition. Original specimens correctly identified (J. H. Price, pers. com.). O. S.

Leptophytum laeve (Strömf.) Adey [*Lithothamnion laeve*]
In deep water, on sheltered and exposed coasts. Found by Børgesen on Bordoy: Haraldssund; Streymoy: Argir; Suduroy: Trongisvágsfjørður and Lopra. (!) S. I.

Lithophyllum incrustans P. Philippi
Intertidal, on *Phymatolithon polymorphum*. Recorded by Jònsson on Viðoy: Viðareiði, and by Børgesen on Suðuroy: Hvalba. O. S.

Lithothamnion glaciale Kjellman
On rocks, stones and shells, subtidal, exposed coasts. Frequent and widely distributed (!) S. I.

Lomentaria articulata (Huds.) Lyngbye
On rocks and stones in the lower intertidal, often accompanying *Corallina,* especially abundant on exposed coasts, where it often occurs in dense mats. Abundant and generally distributed. (!) O. S.

L. clavellosa (Turner) Gaillon
On rocks, stones, and larger algae, especially on the stipes of *Laminaria hyperborea*, lower intertidal and subtidal to 30 m, on very exposed to moderately sheltered shores. Very variable in growth form. Common and widely distributed. (!) O. S. I.

L. orcadensis (Harvey) F. Collins ex Taylor [*L. rosea*]
Near low water and subtidally to 30 m, on rocks and holdfasts of *Laminaria hyperborea.* Widely distributed, frequent on exposed shores. (!) O. S. I.

Membranoptera alata (Huds.) Stackh. [*Delesseria alata*]
Intertidally in clefts, caves and pools, and subtidally on rocks, stones, and epiphytic on *Laminaria hyperborea,* on both sheltered and exposed shores. Common and generally distributed. (!) O. S. I.

Odonthalia dentata (L.) Lyngbye
On rocks, intertidally in shady pools, and subtidally on rocks, stones, and stipes of *Laminaria hyperborea*; on sheltered and exposed shores. Common, widely distributed. (!) O. S. I.

Palmaria palmata (L.) Kuntze [*Rhodymenia palmata*]
On rocks and epiphytic on stipes of *Laminaria hyperborea,* intertidally and in the shallow subtidal, on exposed and sheltered shores. Often forming compact tufted mats intertidally to well above high tide level where streams cascade over a rocky shore. Abundant and widespread. (!) O. S. I.

Peyssonnelia dubyi P. Crouan & H. Crouan
On rocks, stones, shells, and stipes of *Laminaria hyperborea,* subtidally to 20 m, on sheltered to exposed shores. Frequent, widely distributed. (!) O. S.

Phycodrys rubens (L.) Batters [*Delesseria sinuosa*]
Lower subtidal on rocks in shady pools and subtidally to 50 m, on rocks and stones and shells, and epiphytic on stipes of *Laminaria hyperborea,* on sheltered to exposed coasts. In very sheltered conditions occurs as the forma *lingulata*, with narrow spiky fronds drawn out into twisted tendrils, looking quite unlike the typical form. Widespread and abundant. (!) O. S. I.

Phyllophora crispa (Huds.) P. Dixon [*P. rubens*]
On rocks in subtidal, on sheltered and exposed shores. Occasional, in scattered localities, but well grown. Simmons (1896: 266) reported this species from Borðoy: near Klaksvík, but Børgesen was unable to find specimens in this locality, identified Simmons' specimens as young *P. truncata* and hence removed the species from the Faroese flora list, to which it should now be restored. (!) O. S. I.

P. pseudoceranoides (S. Gmelin) Newroth & A. Taylor [*P. membranifolia*]
On rocks intertidally in caves, and in the shallow subtidal on somewhat exposed shores. There is much confusion between young immature specimens of this species and of *P. traillii*. O. S. I.

***P. traillii** Holmes & Batters
In caves and undercuts of cliffs, pools, and shallow subtidal, exposed shores. Occasional. (!) O.

P. truncata (Pallas) Zinova [*P. Brodiaei*]
On stones in shallow subtidal, especially in sheltered conditions. Fairly frequent in widely scattered localities. See *Actinococcus.* (!) O. S. I.

Phymatolithon laevigatum (Foslie) Foslie
On stones and shells subtidally to 20 m, on both sheltered and exposed coasts. Widely distributed. O. S. I.

P. lenormandii (Aresch.) Adey [*Lithothamnion lenormandi*]
Intertidally in pools on both exposed and sheltered shores. Recorded by Børgesen from only two sites, but apparently common and widely distributed. (!) O. S. I.

P. polymorphum (L.) Foslie
On rocks near low water and in shallow subtidal to 20 m. According to Børgesen it occurs luxuriantly in caves to well above sea level. Abundant and widely distributed. (!) O. S. I.

Plocamium cartilagineum (L.) P. Dixon [*P. coccineum*]
On rocks in pools in the lower intertidal, and subtidally on rocks and on stipes and holdfasts of *Laminaria hyperborea*. On exposed to sheltered coasts. Abundant and widely distributed. (!) O. S. I.

Plumaria elegans (Bonnem.) Schmitz
On rocks in the lower intertidal on exposed shores, typically as a mat on shady vertical rock faces, more rarely in pools. Occasional, widely distributed. (!) O. S. I.

Polyides rotundus (Huds.) Grev.
On stones subtidally to 20 m, on sheltered coasts. Locally abundant, widely distributed. (!) O. S. I.

Polysiphonia brodiaei (Dillwyn) Sprengel
On rock intertidally near low water, usually in pools, mainly on exposed shores. Common, widely distributed. (!) O. S.

P. elongata (Huds.) Sprengel
On stones, shells, and other algae in the shallow subtidal to 20 m, on both sheltered and exposed coasts, occasional. Locally abundant, widely distributed. (!) O. S. I.

***P. fibrata** (Dillwyn) Harvey
Lower intertidal amongst *Corallina* in pools on exposed shores. Locally abundant, widely dispersed. (!) O. S.

***P. fruticulosa** (Wulfen) Sprengel
On rocks on exposed shores, and intertidally in pools. Occasional. (!) S.

P. lanosa (L.) Tandy [*P. fastigiata*]
Parasitic on *Ascophyllum*. Widespread and abundant with the host, but absent where moderate wave exposure occurs. (!) O. S. I.

[**P. lepadicola** (Lyngbye) J. Agardh
Recorded by Lyngbye (as *Hutchinsia lepadicola*), but his specimens were found by Børgesen to be creeping filaments of *P. urceolata*].

P. nigra (Huds.) Batters [*P. atrorubescens*]
A few specimens collected by Ostenfeld from 6–8 m subtidally. Suðuroy: Trongisvágsfjørður. Recorded by Lyngbye as occurring in the Faroes, but no specimens were found in his herbarium. O. S.

P. nigrescens (Huds.) Grev.
On rocks and stones in shallow subtidal, on both sheltered and exposed shores. Occasional. (!) O. S. I.

P. urceolata (Lightf. ex Dillwyn) Grev.
On rocks intertidally near low water mark, especially on exposed shores, and subtidally on stipes of *Laminaria hyperborea*, to 20 m. Abundant and generally distributed. (!) O. S. I.

P. violacea (Roth) Sprengel
Epiphytic on *Laminaria*, shallow subtidal, rare, Suðuroy: Trongisvágsfjørður (Ostenfeld and Simmons). Eysturoy: Tórshavn (Holt). O. S.

Porphyra leucosticta Thuret
On rocks and stones at low water level, and in shallow subtidal, on exposed and sheltered shores. Common, widely distributed. (!) O. S.

P. linearis Grev. [*P. umbilicalis* f. *linearis*]
According to Børgesen (1903) found by Lyngbye to be abundant on Suðuroy: Hvalbiarfjørður. Not found by us, but to be expected in winter and spring. O. S. I.

P. miniata (Agardh) Agardh
Free-floating in inner parts of fjords, on rocks and stones and epiphytic, subtidally to 30 m, on exposed and sheltered coasts. Common, widely distributed. (!) O. S. I.

P. purpurea (Roth) Agardh [*P. umbilicalis* f. *laciniata*]
Epiphytic on fucoids intertidally, and in shallow subtidal, on sheltered coasts. Common, widely distributed. (!) O. S. I.

P. umbilicalis (L.) J. Agardh
On rocks intertidally, especially abundant in the swash zone on exposed coasts. Widely distributed. (!) O. S. I.

Porphyropsis coccinea (J. Agardh ex Aresch.) Rosenv. [*Porphyra coccinea*]
Subtidally, epiphytic, mainly on *Desmarestia aculeata,* on exposed and sheltered shores. Common, widely distributed. (!) O. S. I.

Pterosiphonia parasitica (Huds.) Falkenb.
On rocks and shells in shallow subtidal on exposed shores. Common, widely distributed. (!) O. S. I.

Ptilota plumosa (Huds.) Agardh
On rocks and more usually epiphytic on *Laminaria* stipes and holdfasts, subtidal on exposed to relatively sheltered shores to 50 m. Common and widespread. (!) O. S. I.
This species and *P. serrata* are often not easily separable on morphological grounds, and are possibly conspecific.

P. serrata Kütz. [*P. pectinata*]
On rocks and epiphytic on *Laminaria* stipes and holdfasts, subtidal on exposed to relatively sheltered coasts. Occasional, widely distributed. (!) I.

Rhodomela confervoides (Huds.) P. C. Silva [*R. subfusca*]
On stones and shells intertidally, and in shallow subtidal, on sheltered coasts. Occasional. (!) O. S. I.

R. lycopodioides (L.) Agardh
On rocks and stones intertidally, and in shallow subtidal, on sheltered and exposed shores. Common, widely distributed. (!) O. S. I.
This species and *R. confervoides* appear to intergrade morphologically, and are possibly conspecific.

Rhodophysema elegans (P. Crouan & H. Crouan ex J. Agardh) P. Dixon [*Rhododermis elegans*]
On stones and shells in subtidal, occasional. Found by Jønsson on Streymoy: Kaldbaksfjørður and by Børgesen on Suðuroy: Trongisvágsfjørður. I.

Sterrocolax decipiens
See *Ahnfeltia*.

***Trailliella**—tetrasporangial phase of *Bonnemaisonia hamifera*
Epiphytic on various small algae, intertidally in pools, rare. Streymoy: Hoyvík, Eiði. Presumably a relatively recent introduction to the islands, as it appears to be very localized. Known from the Shetland Isles since 1949 (personal record), where it is now abundant and widely distributed. (!) O. S.

CHRYSOPHYTA

Vaucheria coronata Nordst.
In muddy turf, upper edge of sheltered beach, Streymoy: near Hvalvik (det. T. Christensen). Also in mud-filled rock crevices, upper spray zone of moderately exposed shore, Streymoy: near Glyvursnes (Børgesen). (!) O.

PHAEOPHYTA

***Aglaozonia** phase of *Cutleria multifida*
Epiphytic on stipes and haptera of *Laminaria hyperborea,* subtidal to 10 m. Locally common on Eysturoy: Skálafjørður near Strendur and Kumlávik. (!) S.

Alaria esculenta (L.) Grev.

On rocks, lower intertidal to shallow subtidal, mainly on exposed shores but extending some distance into fjords. Abundant and widely distributed. In more sheltered localities the blade is broader and less tattered, approaching the growth-form attributed to *A. pylaii.* (!) O. S. I.

A. pylaii (Bory) J. Agardh

On rocks with moderate shelter, lower intertidal and shallow subtidal. Recorded sparsely from several of the southern islands, but seems doubtfully distinct from *A. esculenta.* Looked for but not found with any certainty by our expedition. I.

Ascophyllum nodosum (L.) Le Jol.

On rocks, midtide level, abundant in sheltered localities, but also found where there was moderate exposure, sometimes even accompanying *Alaria.* Widespread. (!) O. S. I.

Asperococcus fistulosus (Huds.) Hook. [*A. echinatus*]

Found by Simmons epiphytic on *Corallina* on Suðuroy: Hvalbiarfjørður. Epiphytic on fucoids on inner face of harbour wall, Streymoy: Kollarfjørður Harbour, and at Hoyvik in a pool at low water. (!) O. S. I.

***A. turneri** (Sm.) Hook.

On stones and shells, subtidal to 7 m in a sheltered fjord. Eysturoy: Skálafjørður, locally frequent. (!) O. S.

Chorda filum (L.) Stackh.

On pebbles and shells, shallow subtidal to 4 m in sheltered localities, especially near heads of fjords. Widespread and locally abundant. (!) O. S. I.

Chordaria flagelliformis (Müll.) Agardh

On stones and epiphytic, in lower intertidal pools and shallow subtidal to 10 m on sheltered to moderately exposed shores. Common and widespread. (!) O. S. I.

Cladostephus spongiosus (Huds.) Agardh

Found by Børgesen only in lower intertidal rock pools on an exposed rock platform on Eysturoy: near Gjógv. O. S. I.

Cutleria multifida (Sm.) Grev.

See *Aglaozonia.*

Desmarestia aculeata (L.) Lamouroux

On rocks and stones, more rarely epiphytic, on exposed and sheltered coasts, subtidal to 20 m. Often in large detached masses on sand or mud in very sheltered localities. Widespread and abundant. (!) O. S. I.

D. ligulata (Lightf.) Lamouroux

On rocks and epiphytic on *Laminaria* stipes, rarely encountered attached, occasional as drift specimens. Our expedition found only one small tattered specimen, growing attached in the shallow subtidal. Recorded from Eysturoy, Suðuroy and Streymoy. Rex (1970) records it as occasional on the stipes of *Laminaria hyperborea* on Streymoy: Hoyvik. (!) O. S. I.

D. viridis (Müll.) Lamouroux

On stones and rocks, more rarely epiphytic, on exposed to moderately sheltered shores, subtidal to 20 m. Abundant and widespread. (!) O. S. I.

Desmotrichum undulatum (J. Agardh) Reinke

Found once by Børgesen in shallow water along with *Cystoclonium purpureum* at Streymoy: Sundini. S.

***Dictyosiphon chordaria** Aresch.

A specimen possibly belonging to this species was collected in shallow non-tidal water on Eysturoy: at the head of Skálafjørður. (!) O. S. I.

D. ekmanii Aresch. [*D. Ekmani*]
Epiphytic on *Scytosiphon,* shallow subtidal on sheltered shore, found only on Borðoy: Klaksvík by Børgesen. I.

D. foeniculaceus (Huds.) Grev. (includes *D. hippuroides*)
Epiphytic on *Chordaria flagelliformis* in pools and shallow subtidal on sheltered shores. Common, widely distributed. (!) O. S. I.

Ectocarpus fasciculatus Harvey
On rocks and epiphytic on various algae, intertidal and shallow subtidal, on exposed and sheltered shores. Common and widespread. (!) O. S. I.

E. siliculosus (Dillwyn) Lyngbye [Includes *E. confervoides, E. dasycarpus*]
On rocks and shells and epiphytic on various algae, intertidal and subtidal to 10 m, on exposed and sheltered shores. Common and widespread. (!) O. S. I.

[**Elachista flaccida** (Dillwyn) Aresch.
Recorded by Lyngbye as rather rare on *Fucus vesiculosus,* but his herbarium specimens (fide Børgesen) are *E. fucicola.* Recorded by Simmons on *Himanthalia elongata* near Tórshavn (Streymoy) and on *Fucus vesiculosus* in Hvalbiarfjørður (Suðuroy). It seems unlikely that any of these are reliable records. O. S.]

E. fucicola (Velley) Aresch.
Epiphytic on intertidal fucoids on exposed and sheltered shores. Very common and widespread. (!) O. S. I.

E. scutulata (Sm.) Aresch.
On receptacles of *Himanthalia.* Common and widely distributed. (!) O. S.

Eudesme virescens (Carmich. ex Harvey) J. Agardh [*Castagnea virescens*]
Found by Børgesen on stones in shallow subtidal in sheltered locality, Streymoy: between Hósvik and Hvalvik, and by us in sheltered lower intertidal pools and shallow subtidal on Eysturoy and Streymoy. (!) O. S. I.

[**Fucus ceranoides** L.
Recorded by Lyngbye, but no Faroese specimens are to be found in his herbarium (fide Børgesen). No other phycologist has reported finding this species in the Faroes. O. S. I.]

F. distichus L. subsp. **distichus** [*F. inflatus* f. *linearis*]
On rocks in high level pools on exposed coasts. Found by Børgesen only on Suðuroy: near Fámjin. S.

F. distichus subsp. **anceps** (Harvey & N. Ward ex Carruth.) H. Powell [*F. inflatus* f. *disticha*]
On rocks intertidally, often well above sea-level on exposed shores. Widely distributed. (!) O. S. I.

F. distichus subsp. **edentatus** (Bach. Pyl.) H. Powell [*F. inflatus* f. *edentata*]
On rocks, shallow subtidal, on sheltered shores, often with reduced salinity. Very variable in size and growth form. Abundant and widespread. (!) O. S. I.

[**F. serratus** L.
Reported by Landt as widespread at the base of cliffs, but no other investigator records finding this species, so the record would seem to be an error. O. S. I.]

F. spiralis L.
On rocks, intertidally, on sheltered to exposed shores. With increased exposure plants become dwarfed (f. *nana* Kjellman), and can grow up to 5 m above high water mark (fide Børgesen) and may also occur in high level pools. Abundant and widespread. (!) O. S. I.

F. vesiculosus L.
On rocks and stones at midtide level to shallow subtidal, on sheltered shores, often almost to the heads of fjords in brackish water. Very common and widespread. (!) O. S. I.

Giffordia granulosa (Sm.) Hamel [*Ectocarpus granulosus*]

Epiphytic on *Laminaria* blades, subtidal at 4–6 m on sheltered shores. Viðoy: near Hvannasund (Jønsson). Suðuroy: Trongisvágur (Ostenfeld). Eysturoy: Eiði. (!) O. S. I.

G. hincksiae (Harvey) Hamel [*Ectocarpus Hincksiae*]

Epiphytic on larger algae, intertidal and subtidal to 20 m, typically on exposed coasts. Common and widespread. (!) O. S. I.

Halidrys siliquosa (L.) Lyngbye

Found attached in shallow subtidal (2 m) in Eysturoy: Skálafjørður near Glyvrar, and in drift in several localities, but would seem to be uncommon and very localized. Our expedition searched for it fruitlessly in the recorded sites. O. S.

Halosiphon tomentosus (Lyngbye) Jaasund [*Chorda tomentosa*]

On rocks, pebbles and shells, subtidal to 10–12 m, associated with *Alaria, Laminaria* spp. and other large seaweeds. Borðoy: Ánir. Eysturoy: Mölin and Eiði. Streymoy: Sundini (Rex). I.

Hecatonema foecundum (Strömf.) Lois.

Forming dense mat on blade of *Laminaria hyperborea*; found by Børgesen at Tórshavn. I.

Herponema velutinum (Grev.) J. Agardh [*Ectocarpus velutinus*]

Reported by Simmons on *Himanthalia* in Hvalbiarfjørður (Suðuroy), but not found by Børgesen on two original *Himanthalia* specimens of Simmons which did, however, bear *Elachista scutulata*. S.

Himanthalia elongata (L.) Gray

On rocks at low tide level on exposed shores or in strong currents; on very exposed shores often well above low tide level. Common and widespread. (!) O. S.

Isthmoplea sphaerophora (Carmich. ex Harvey) Kjellman

Epiphytic on various intertidal algae on exposed shores. Common and widespread. (!) O. S. I.

Laminaria digitata (Huds.) Lamouroux

On rocks, intertidal to subtidal, on sheltered to exposed coasts. Common and widespread. (!) O. S. I.

L. faeroensis Børg. (=*L. saccharina* forma?)

On stones, rocks, and shells in subtidal to 20 m, in very sheltered localities such as harbours and heads of fjords. Abundant and widespread. For taxonomic status see Kain (1976). (!) S.

L. hyperborea (Gunnerus) Foslie

On rocks, subtidal to 40 m, exposed to moderately sheltered shores, forming dense forests. Widespread and abundant. (!) O. S. I.

L. saccharina (L.) Lamouroux

On rocks and stones or epiphytic on large algae, in pools in lower intertidal and in subtidal to 20 m; on exposed to sheltered coasts. Common and widespread. (!) O. S. I.

Laminariocolax tomentosoides (Farlow) Kylin [*Ectocarpus tomentosoides*]

Partly endophytic in stipes and blades of *Laminaria* spp., forming short matted growth. Common and fairly widespread. O. S.

Leathesia difformis (L.) Aresch.

On rocks or epiphytic on *Corallina,* intertidal, mainly in sheltered situations. Common and widespread. (!) O. S. I.

Leptonematella fasciculata (Reinke) P. C. Silva [*Leptonema fasciculata*]

Found by Børgesen on Eysturoy: Glyvrar and Fuglafjørður. O. S. I.

Litosiphon filiformis (Reinke) Batters [*Pogotrichum filiforme*]

Epiphytic on blades of *Laminaria saccharina,* often forming dense mats. Found by Børgesen on Streymoy: Tórshavn and Vágar: Miðvagur, and by us on Eysturoy: Skálafjørður. (!) S. I.

L. laminariae (Lyngbye) Harvey

Epiphytic on *Alaria* blades, often forming a dense mat. Frequent, widely distributed. (!) O. S.

Microspongium globosum Reinke [*Myrionema globosum*]

Epiphytic on *Himanthalia* and other large algae, forming small cushions or mats, intertidal and shallow subtidal. Found by Børgesen on Streymoy and Suðuroy. O.

Mikrosyphar polysiphoniae Kuck.

Endophytic in *Polysiphonia urceolata* and *Callithamnion hookeri*, intertidal and shallow subtidal. Found by Børgesen on Eysturoy: Oyri and Streymoy: Hoyvík and Kvívík. S. I.

M. zosterae Kuck.

Epiphytic on *Zostera marina*, often forming rather large pseudoparenchymatous patches. Found by Børgesen on Suðuroy: Vágsfjørður.

Myrionema aecidioides (Rosenv.) Sauvageau

On blades of *'Laminaria faeroensis'*. Found at Eysturoy: Skálafjørður, and Streymoy: Hvalvik by H. Jønsson. S. I.

M. corunnae Sauvageau

Forming short dense cushions on *Laminaria digitata* blades. Found by Børgesen on Suðuroy: Fámjin. I.

M. faeroense Børg.

On *Palmaria palmata*, in small dense mats, often with *Microspongium globosum*, on Streymoy: near Tórshavn, the type locality. Not found or investigated since first described by Børgesen.

M. speciosum Børg.

On conceptacles of *Himanthalia*, forming short dense mats, often with *Microspongium globosum*, on exposed coasts on Suðuroy: Vágseiði, the type locality. Not found or investigated since first described.

M. strangulans Grev. [*M. vulgare*]

Epiphytic on *Monostroma fuscum*, and various spp. of the Ulvaceae. Streymoy: between Hósvik and Hvalvik. Eysturoy: Skálafjørður near Strendur (!) and Kumlávik (!). (!) O. S. I.

***Myriotrichia clavaeformis** Harvey

Epiphytic on *Scytosiphon* in lower intertidal on Streymoy. (!) O. S.

Pelvetia canaliculata (L.) Dcne & Thuret

On rocks about high tide level in sheltered situations. Common but rather sporadic, often of minute size. (!) O. S. I.

Petalonia fascia (Müll.) Kuntze [*Phyllitis fascia*]

Intertidal on rocks and stones and epiphytic, often in pools. On exposed and sheltered shores. Common. (!) O. S. I.

P. zosterifolia (Reinke) Kuntze [*Phyllitis zosterifolia*]

On rocks intertidally on exposed to fairly sheltered coasts. Rather rare and local. I.

Petroderma maculiforme (Wollny) Kuck.

Forming small brown patches on smooth rock surfaces near high tide level. Streymoy: Saksun (Børgesen). I. S.

Phaeostroma parasiticum Børg.

Epiphytic on blade of *'Laminaria faeroensis'* in shallow sheltered subtidal. Streymoy: between Hósvik and Hvalvik (Børgesen).

Pilayella littoralis (L.) Kjellman [*Ectocarpus littoralis*]

On rocks and epiphytic, intertidal and shallow subtidal, growing in damp clefts to 2 m or more above high tide level. Abundant and widespread. (!) O. S. I.

Pleurocladia lacustris Braun [*Pilinia.maritima*]
Found by Børgesen on rocks at high tide level, intermingled with crustose blue-green algae, on Sandoy: near Sandur.

***Pseudolithoderma extensum** (P. Crouan & H. Crouan) S. Lund [*Lithoderma fatiscens*]
On stones and shells subtidally, 1–40 m, on exposed and sheltered shores. Fairly widely distributed. (!) S. I.

Punctaria latifolia Grev.
On rocks and epiphytic on large algae in the lower intertidal and shallow subtidal on sheltered coasts. Fairly widely distributed. (!)

P. plantaginea (Roth) Grev.
On stones in shallow subtidal in very sheltered situations. (!) O. S. I.

Ralfsia clavata (Harvey) P. Crouan & H. Crouan
On rocks about 3 m above high water mark on Suðuroy: near Fámjin; a small quantity of an alga presumed by Børgesen to belong to this species. O. S. I.

R. verrucosa (Aresch.) J. Agardh
On rocks intertidally and in shallow subtidal, especially in pools, on sheltered and exposed coasts. Abundant and widely distributed. (!) O. S. I.

[*Saccorhiza polyschides* (Lightf.) Batters
Recorded from the Faroes by Landt, but not found by Børgesen or other investigating phycologists. It is, however, common in the Shetland Isles. O. S.]

Scytosiphon lomentaria (Lyngbye) Link [*S. lomentarius*]
On rock intertidally and in shallow subtidal, exposed to sheltered shores, able to withstand low salinities. Abundant and widespread. (!) O. S. I.

Sorapion kjellmanii (Wille) Rosenv.
Epiphytic on *Chaetomorpha melagonium*. Found by Børgesen on Streymoy: near Tórshavn.

Sphacelaria caespitula Lyngbye
On stipes of *Laminaria,* rare. Eysturoy: Nes (Lyngbye). Streymoy: Kvívík (Børgesen). I.

S. cirrosa (Roth) Agardh [*S. cirrhosa*]
Epiphytic on *Desmarestia aculeata* and *Chaetomorpha melagonium* on exposed and sheltered shores. On Svínoy and on Suðuroy: Vágsfjørður (Jónsson). On *Cladophora rupestris,* in midtide pools, on Streymoy: Hoyvik (!) , Tórshavn (!). (!) O. S. [I?].

S. nana Naeg. ex Kütz. [*S. britannica*]
On damp rocks around high tide level, especially in caves and clefts, forming a dark brown mat, on fairly exposed shores. Found by Børgesen on Streymoy: Kvívík and Glyvursnes. O. S. [I?].

S. plumosa Lyngbye [*Chaetopteris plumosa*]
On cobbles, subtidal 4–6 m, Eysturoy: Ánir (!), Skálafjørður (!). Specimens in Rostrup's herbarium said to have been found on Faroes by Mr Randtopp of Tórshavn (fide Børgesen). (!) O. S. I.

S. rigidula Kütz. [*S. furcigera*]
On a *Laminaria* stipe, subtidal, 6–8 m, on fairly exposed shore. Found by Børgesen at Tórshavn, det. as *S. furcigera* by Sauvageau, Eysturoy: Ánir (!), Skàlabotnur (!). (!) O. S.

Spongonema tomentosum (Huds.) Kütz. [*Ectocarpus tomentosus*]
Epiphytic on the larger algae, intertidal on both exposed and sheltered coasts. Common and widespread. (!) O. S. I.

***Stictyosiphon griffithsianus** (Le Jolis) Holmes & Batters
Epiphytic on *Palmaria palmata,* Streymoy: Kirkjubøur. (!) S.

S. tortilis (Rupr.) Reinke
On stones and epiphytic on *Chordaria flagelliformis,* in shallow subtidal on sheltered shores, often where salinity is reduced. Found by Børgesen on Eysturoy and Suðuroy, but probably much more widely distributed. O. S. I.

Streblonema stilophorae (P. Crouan & H. Crouan) Hamel [*Ectocarpus Stilophorae*]
Found by Børgesen in the sorus of a *Laminaria* plant in Tórshavn. I.

Ulonema rhizophorum Foslie
Epiphytic on *Dumontia contorta* at mid to lower shore levels. Esturoy: near the inner end of Skálafjørður. (!) O.S.

Waerniella lucifuga (Kuck.) Kylin [*Ectocarpus lucifugus*]
On rocks in cracks and fissures near high tide level, intermixed with *Rhizoclonium.* Found at Viðoy: Viðvik, and Borðoy: Klaksvik, both, by Jønsson. Viðoy (!). (!) S.

CHLOROPHYTA

Acrochaete repens Pringsh.
Found in old fronds of *Chorda filum* by H. Jønsson on Eysturoy: Skálafjørður. Streymoy: Hvalvik. I.

Blidingia minima (Naeg. ex Kütz.) Kylin [*Enteromorpha intestinalis* var. *minima*]
On exposed shores in spray zone. Abundant and widespread. Eysturoy: Gjógv (det. Burrows) (!). (!) O. S. I.

Bolbocoleon piliferum Pringsh.
Found by Børgesen between cortical cells of *Petalonia fascia* and *Scytosiphon lomentaria* on Mykines and Streymoy: Sundini. O. S. I.

Bryopsis plumosa (Huds.) Agardh
On rocks in deep pools and in shallow subtidal. Widely distributed, but rare and sporadic (!). Svinoy: Svínoyareiði (!). Streymoy: Tórshavn to Hoyvik (!). (!) O. S. I.

***Capsosiphon fulvescens** (Agardh) Setch. & N. Gardner
Amongst vascular plants at high tide level at the head of a fjord. Locally common. Eysturoy: Skálafjorður. (!) O. S. I.

Chaetomorpha capillaris (Kütz.) Børg. [*C. tortuosa*]
On rocks or loose lying or entangled amongst other algae, in pools at high tide level. In sheltered habitats. Widely distributed (!). Streymoy: Hedfjordur, Kirkjubøur, Argir (det. Burrows) (!). (!) O. S. [I?]

C. melagonium (F. Weber & Mohr) Kütz.
On rocks and epiphytic, in intertidal pools and subtidal, exposed to sheltered shores. Very common (!). Streymoy: Argir (!). (!) O. S. I.

***Chlorochytrium cohnii** E. Wright
Eysturoy: Skálafjørður, subtidal in 'Schizonema' tubes (det. Burrows) (!). (!) O. S. I.

C. inclusum Kjellman—non-specific phase in life-history of *Spongomorpha* spp.
Endophytic in various red algae. Widely distributed. (!) O. S. I.

[**Cladophora fracta** (Müll. ex Vahl) Kütz.
Recorded by Rostrup as a common Faroese species, but Børgesen considered this a case of misidentification, and no reliable herbarium material of this species from the Faroes exists. It was not found by either Børgesen or us. S.]

C. rupestris (L.) Kütz.
On rocks and stones intertidally in pools and in shallow subtidal, on exposed and sheltered coasts. Abundant and widespread (!). Streymoy: Argir (det. Burrows) (!). Eysturoy: Skálafjørður (det. Burrows) (!). (!) O. S. I.

C. sericea (Huds.) Kütz. [*C. gracilis*]
In midtide to high tide level rock pools on moderately exposed to sheltered shores. Frequent and widespread. Eysturoy: Skálafjørður, Raktangi (det. Burrows) (!), Strendur. Streymoy: Argir (det. Burrows) (!). Viðoy: Hvannasund (det. Burrows) (!). (!) O. S. I.

Codiolum gregarium—phase in life-history of *Ulotrichales* spp.
On rocks near high tide level on sheltered and exposed coasts. Frequent and widespread. I.

C. pusillum—phase in life-history of *Ulotrichales* spp.
Found by Lyngbye on rocks at high tide level on Suðuroy: Hvalba. Eysturoy: Elduvík. I.

Derbesia marina (Lyngbye) Solier
On rocks, *Corallina, Laminaria* stipes and worm-tubes, subtidally from extreme low tide level to 20 m. Not uncommon, but easily overlooked. See *Halicystis.* (!) S. I.

Enteromorpha clathrata (Roth) Grev.
In sheltered shallow subtidal locations, often free-floating in large tangled masses. Locally common. O. S. I.

E. compressa (L.) Grev. [*E. intestinalis* var. *compressa*]
On rocks or epiphytic, intertidal, often in pools. Common and generally distributed. (!) O. S. I.

E. intestinalis (L.) Link
On rocks and epiphytic, intertidal and above, and in shallow subtidal, on exposed to fully sheltered shores, from fully saline to virtually freshwater habitats. Abundant and widespread. (!). Streymoy: Argir (det. Burrows) (!), Kaldbaksfjørður (det. Burrows) (!). Eysturoy: Raktangi (det. Burrows) (!). (!) O. S. I.

E. linza (L.) J. Agardh
On rocks and stones on open shores near low tide level, in pools and in shallow subtidal. Common and widespread (!). Viðoy: Hvannasund, near causeway (!). Eysturoy: Skálafjørður, Raktangi (det. Burrows) (!), Strendur. (!) O. S. I.

E. prolifera (Müll.) J. Agardh [*E. intestinalis* var. *prolifera*]
On rocks or detached, intertidal in pools and subtidal, in sheltered localities such as the heads of fjords, often growing in virtually freshwater. Locally common. Eysturoy: Gjógv (det. Burrows) (!). (!) O. S. I.

*__E. torta__ (Mert.) Reinb.
In shallow subtidal, 3–4 m, on holdfast of '*Laminaria faeroensis*', with *Rhizoclonium riparium, Erythrotrichia carnea,* and *Polysiphonia urceolata*. Eysturoy: Skálafjørður, Strendur. (!) O. S.

Gomontia polyrhiza (Lagerh.) Bornet & Flah.
Endophytic in mollusc shells, subtidal to 30 m. Common and widespread. I.

Halicystis ovalis—haploid phase of *Derbesia marina.* [*Valonia ovalis*]
On rocks and shells, extreme low tide level and subtidal. Found at various sites by Lyngbye. Sandoy: Trøllkonufinger (!). S.

Monostroma fuscum (Postels & Rupr.) Wittr.
On rocks and stones and epiphytic, in runnels and subtidally to 20 m. Common and widespread (!). Streymoy: Argir (det. Burrows) (!). (!) O. S. I.

M. grevillei (Thuret) Wittr.
Epiphytic, especially on *Corallina,* or on rocks, in shallow pools on sheltered to moderately exposed shores. Common and widespread. (!) O. S. I.

M. undulatum Wittr.
Epiphytic, especially on *Corallina,* or on rocks, lower intertidal and shallow subtidal. Widely distributed. O. I.

Ostreobium queckettii Bornet & Flah.

Endophytic in mollusc shells in subtidal to 50 m. Common and widely distributed. O. S.

Percursaria percursa (Agardh) Rosenv.

On flat sheltered shores at high tide level, with *Vaucheria.* Found by Børgesen on Streymoy: Sundini. O. S. I.

Phaeophila wittrockii (Wille) R. Nielsen [*Endoderma Wittrockii*]

In cell walls of various brown algae. Widely distributed. S. I.

Prasiola crispa subsp. **marina** Børg.

On steep rocks on exposed coasts. Common. S. I.

P. crispa subsp. **terrestris** (Roth) Børg.

On rocks and shady soil just above high tide level in the spray zone.

P. furfuracea (Mert.) Menegh.

On rocks in surge zone of exposed coasts. Found by Børgesen on Streymoy: Tinganes. I.

P. stipitata Suhr

On rocks and stones at high tide level and above, especially with high nitrate levels from bird droppings, etc. Abundant and widespread. (!) O. S. I.

Pringsheimiella scutata (Reinke) Marchew.

Found by Børgesen epiphytic on various algae and on *Zostera marina*, intertidally and in shallow subtidal, on exposed and sheltered shores. Widely distributed. O. S. I.

Pseudopringsheimia confluens (Rosenv.) Wille [*Ulvella confluens*]

Found by Børgesen epiphytic on *Gigartina* intertidally on exposed shores on Streymoy: Velbastaður.

P. fucicola (Rosenv.) Wille [*Ulvella fucicola*]

Found by Børgesen on *Fucus distichus* on Suðuroy: Tvøroyri. S. I.

Rhizoclonium riparium (Roth) Harvey

On rocks near high tide level and in the spray zone, forming large thick mats, often associated with percolating freshwater. Common and widely distributed. Eysturoy: Skálafjørður, subtidal (det. Burrows) (!). (!) O. S. I.

Spongomorpha aeruginosa (L.) Hoek [*S. lanosa*]

On *Cladophora rupestris* in intertidal pools and shallow subtidal. Found sparsely by Børgesen on Streymoy: between Hósvik and Hvalvik (!) and on Eysturoy: Kumlávik (!), Raktangi (det. Burrows) (!). (!) O. S. I.

S. arcta (Dillwyn) Kütz. [*Acrosiphonia albescens.* Probably includes *A. binderi, A. flagellata,* and *A. incurva*]

On rocks and stones and epiphytic, near low tide level and in shallow subtidal, forming dense mats, on exposed and sheltered shores, or occurring in sheltered areas as large detached masses. Common and widely distributed. Eysturoy: Raktangi (det. Burrows) (!), head of Skálafjørður (det. Burrows). Streymoy: Argir (det. Burrows) (!). (!) O. S. I.

***S. sonderi** Kütz.

Eysturoy: head of Kaldbaksfjørður (det. Burrows). (!) S.

Ulothrix consociata Wille

On stones, intertidal, in sheltered localities. Found by H. Jønsson on Suðuroy: Trongisvágur. S. I.

U. flacca (Dillwyn) Thuret

On rocks and epiphytic on the larger algae, intertidal, on exposed and sheltered shores. Common. O. S. I.

U. pseudoflacca Wille
Epiphytic on various algae, intertidal, on exposed and sheltered shores. Common. S. I.

Ulotrichales spp.
See *Codiolum gregarium* and *C. pusillum*.

Ulva lactuca L.
On rocks and stones, and epiphytic on the larger algae, lower intertidal and shallow subtidal to 20 m, on sheltered and exposed shores. Common. Streymoy: Hoyvik (!), Tórshavn (!). Eysturoy: Raktangi (det. Burrows) (!). (!) O. S.

U. rigida (Agardh) Thuret
In rock pools and shallow subtidal. Eysturoy: Skálafjørður (det. Burrows) (!), Raktangi (det. Burrows) (!). (!) O. S. I.

Urospora mirabilis Aresch.
On rocks and stones near high tide level on exposed coasts. Common and widespread.

***U. penicilliformis** (Roth) Aresch.
On exposed intertidal rocks, Streymoy: Argir. (!) S. I.

U. wormskioldii (Mert.) Rosenv.
On rocks about high tide level on exposed to sheltered shores. Found by Børgesen at various sites on Eysturoy and Streymoy. (!) I.

4. Conclusions

This investigation covered only a limited period of the year, so doubtless missed many of the seasonally ephemeral species. Attention was concentrated on macroscopic species, and clearly there is considerable scope for a thorough investigation of, for instance, the microscopic brown algae, particularly the species described by Børgesen from the Faroes. The crustose corallines, a particularly difficult group to study, require more consideration than we could give them, and the inner parts of the fjords and the two large southern islands, Sandoy and Suðuroy, would almost certainly repay concentrated attention.

Nevertheless, many interesting conclusions can be drawn from this study. Firstly, it is clear that Børgesen's investigations were very thorough, that he missed or misinterpreted little, and that his analyses of the floristic units are sound. Secondly, the marine flora has changed little since his day, with few introductions of any significance. This is presumably due to the unfavourable current pattern illustrated in Fig. 2, which gives little help in bringing viable algal propagules from elsewhere, though it is perhaps strange that the flourishing Faroese shipping communications have not helped to introduce new species (except, perhaps, the *Trailliella*-phase of *Bonnemaisonia hamifera*).

Thirdly, not only is the seaweed flora considerably poorer than that of the neighbouring Shetland Isles, but the cut-off is in many cases very abrupt. Several species which are abundant and widespread in the Shetland Isles have either not been recorded from the Faroes at all or are apparently rare and local. These include the following:

Apoglossum ruscifolium (Turner) J. Agardh
Gelidium pusillum (Stackh.) Le Jolis
Griffithsia corallinoides (L.) Batters
Halarachnion ligulatum (Woodw.) Kütz.
Hypoglossum woodwardii Kütz.
Laurencia pinnatifida (Huds.) Lamouroux
Polyneura gmelinii (Lamouroux) Kylin
Rhodophyllis divaricata (Stackh.) Papenf.
Scinaia forcellata Biv.
Desmarestia ligulata (Lightf.) Lamouroux

Fucus serratus L.
Halidrys siliquosa (L.) Lyngbye
Saccorhiza polyschides (Lightf.) Batters

Alien species which have been firmly established in the Shetland Isles for several decades at least, yet so far are unrecorded for the Faroes, include *Colpomenia peregrina* Sauvageau and *Codium fragile* subsp. *atlanticum* (A. Cotton) P. C. Silva.

Altogether nine Cyanophyta, 95 Rhodophyta, one Chrysophyta, 74 Phaeophyta and 44 Chlorophyta are recorded for the Faroes, making 223 species. This compares with 301 species reported from the neighbouring Shetland Isles (Irvine, 1980).

A study of past records indicates that some species fluctuated considerably in their distribution and populations: it may be that these species are indeed on the outer fringes of their range, and periodically suffer a catastrophic decline, recovering perhaps very slowly indeed, due to the lack of readily available sources of replenishing propagules. *Laurencia pinnatifida, Desmarestia ligulata, Halidrys siliquosa,* and perhaps *Dilsea carnosa*, may belong to this category. More long term studies of the marine algae of these isolated islands would be highly desirable.

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Seaweeds of the Faroes
2: Sheltered fjords and sounds

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Synopsis

Some results of an international expedition to the Faroes during the summer of 1980 are included. The occurrence and distribution of benthic marine algae in sheltered fjords and sounds are described. Comparisons are made with the results of previous surveys undertaken by Børgesen at the beginning of this century, and with the descriptions of vegetation presented recently for fjords in the Shetlands, Norway and Iceland. A reduced 'fjord effect' was seen in Faroese fjordic systems. The artificially divided Hvannasund did not show a 'fjord effect', but was an inlet of the sea.

1. Introduction

The Faroes lie in the northern Atlantic Ocean between the Shetland Islands and Iceland. The island group comprises 17 inhabited and numerous small uninhabited islands and reefs. The main islands are separated by narrow sea-passages and the coastline is deeply indented with fjords.

The present work was undertaken in July 1980 during a wider survey of the seaweeds of the Faroes (Irvine, 1982; Price & Farnham, 1982). The seaweed vegetation has been studied on only a few previous occasions. Børgesen (1902, 1904, 1905) and Børgesen & Jónsson (1905) undertook a comprehensive survey, which included both littoral and sublittoral habitats throughout the island group. More recent, but less detailed, studies which mention algae were

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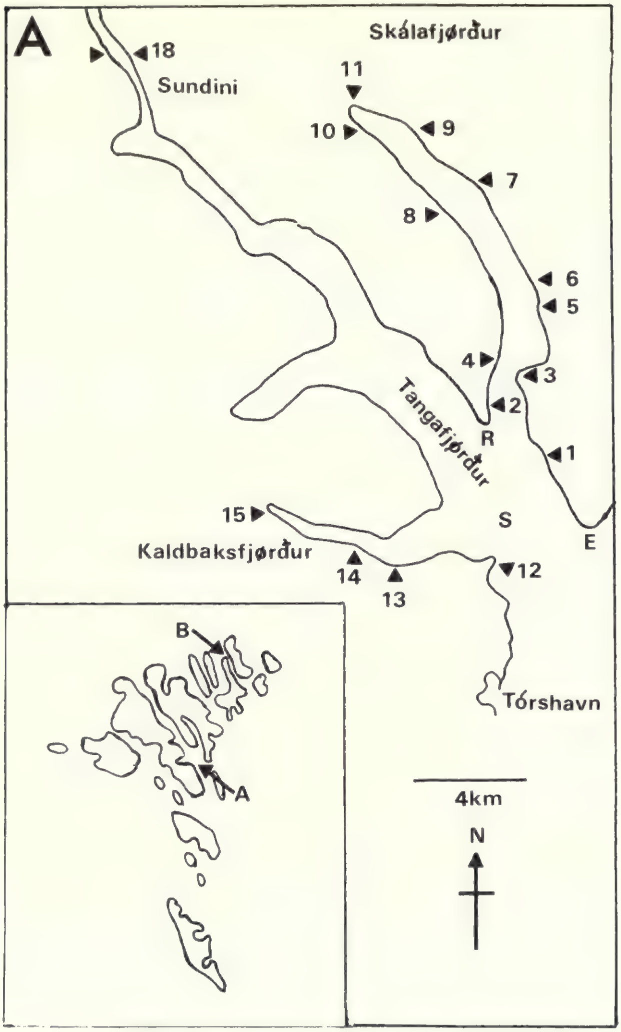

Fig. 1 Maps of the Faroes (inset) and the Skálafjørður/Kaldbaksfjørður region (A on inset). Hvannasund is indicated B on inset. Numbers represent sites investigated (see text). Letters R = Raktangi; S = Storafles; E = Eystnes.

undertaken by Rex (1970), Holt (1975), Jóhansen (1979), and Crothers (1981). Børgesen's (1905) publication included ecological descriptions of the algal associations in sheltered waters.

The main area selected for the present investigation was Skálafjørður, on the southern part of Eysturoy (Fig. 1). Other sites were visited for comparison in Kaldbaksfjørður (Streymoy), Hvannasund (Viðoy) and Sundini, as well as the passage between Eysturoy and Streymoy (Fig. 1).

2. Areas of investigation

Skálafjørður is a narrow, undivided sea inlet approximately 15 km in length and almost bisects the southern part of Eysturoy; this fjord opens to the Atlantic Ocean via Tangafjørður. The surrounding hills are drained by a number of small streams and rivulets, draining into the fjord. A larger river enters at the head-end. The foreshore surrounding Skálafjørður is narrow and formed of hard, basaltic rocks and boulders.

Maximum depths of 72 m have been charted for the region of the fjord near Strendur and Glyvrar; elsewhere, in the middle regions, depths vary between 50 m and 60 m. At the head end and at the entrance to the fjord the maximum depths are less than 20 m. In many places the sea shore shelves abruptly into the shallow sublittoral zone and thereafter slopes more gradually. The slope of the sea bed varies little throughout the fjord. At most sites the sea bed consists of bedrock or boulders in the shallow sublittoral*; at greater depths there is an area of small boulders stones and shells which in the deepest waters merges into an extensive area of fine silt.

The *Admiralty Tide Tables* record no appreciable tides for Skálafjørður; during our periods of field work, however, a rise and fall of between 0·5–1 m was observed at the seaward end of the fjord. At the landward end, the tidal effect was negligible, although a fall of 0·4–0·5 m was noted on the harbour wall at Skálabotnur.

Hydrological data for Skálafjørður are sparse, but Børgesen (1905) gave a general account of the marine physical environment for the Faroes. This included measurements of surface salinities taken at the head-end near the mouth of the fjord, which showed no significant reductions; temporary, local reductions presumably occur following periods of heavy rain. The surface water temperature (July 1980) was 12°C and this parameter may also vary during strong run-off. As Børgesen (1905) indicated, the temperature of the open sea varies little throughout the year.

Kaldbaksfjørður forms an indentation to the eastern side of Streymoy and opens to the Atlantic Ocean via Tangafjørður; it lies almost opposite the entrance to Skálafjørður. This fjord is smaller (approximately 7 km in length) than Skálafjørður, and maximum depths of 60 m have been charted near its entrance; maximum depth decreases to 30 m near the head-end. The latter comprises an extensive foreshore of shingle and mud, traversed by a river and estuary. This foreshore extends for a considerable distance under shallow standing water of less than 0·5 m; it then shelves abruptly to the deeper sublittoral. Kaldbaksfjørður is otherwise fringed by a narrow foreshore of rock or boulders. Although the *Admiralty Tide Tables* again state there to be no appreciable tidal movement, a range of approximately 1 m was observed at the entrance of the fjord; by two-thirds of the way into Kaldbaksfjørður the range had decreased to a few centimetres, and at the head-end there was little tidal movement at all. Although rivers and streams enter, the waters were fully saline throughout. Presumably, local reductions in salinity at the head-end follow periods of rainfall.

Hvannasund is a narrow channel separating the islands of Viðoy and Borðoy. The channel has recently been blocked at its narrowest point by a causeway constructed of large boulders. This man-made isthmus has artificially divided Hvannasund into two fjord-like arms; the northern arm was selected for investigation. The sound is surrounded by high hills and is fringed by a narrow, steeply sloping, and often almost vertical, rocky foreshore which continues into the sublittoral. Maximum depths of 80 m have been charted for the outer reaches of Hvannasund. At the inner end, the foreshore is more gently sloping and maximum depths are less than 15 m. The waters of the sound remain saline throughout.

Sundini is the narrow sea passage (sound) which separates Streymoy from Eysturoy.

3. Materials and methods

The intertidal and sublittoral vegetation was recorded by direct observations at eleven sites in Skálafjørður, four sites in Kaldbaksfjørður, two sites in Hvannasund and one area in Sundini. At intertidal sites species were listed, and the shore level at which they occurred, recorded. Subtidal bands of vegetation were identified by eye during scuba diving, samples of algae and substratum being taken from each band and brought back to the laboratory for checking. Vertical extents of sublittoral bands were recorded by depth gauge.

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* Shore zone terminology follows Lewis (1964).

4. Sites investigated

Skálafjørður

1. Nes near Toftir
Situated just out of the fjord on the eastern side of Eysturoy where conditions are fairly exposed. The intertidal comprised a narrow foreshore of rocks and boulders with occasional pools. A concrete quay was built over part of the foreshore. The foreshore of bedrock sloped into the sublittoral and was overlain at a depth of 3 m by a substrate of boulders and stones. At 10 m the substrate was of boulders, gravel, and horse-mussels (*Modiolus modiolus* L.); at 15 m there were fewer *Modiolus* and at 16 m (100 m offshore) the substrate was mainly gravel and mud.

2. Kumlavik
Located on the western side of the fjord near its confluence with Tangafjørður. The intertidal comprised a small rocky headland which continued into the sublittoral to a distance of 80 m offshore (10 m depth). At greater depths the sea bed was covered by gravel and sand.

3. Saltnes
Situated on the eastern shore of the fjord 2 km inland of the entrance. At this point the fjord was less than 1 km wide. A narrow rocky foreshore gave way in the shallow sublittoral to an extensive area of gravel and shells. At a distance of 50 m offshore (10 m depth) the sea bed was formed of mud and silt.

4. Strendur
Situated on the western side of the narrows in the fjord, opposite site 3. The narrow rocky foreshore sloped into the sublittoral to a depth of 3 m. At greater depths the sea bed comprised gravel and sand deposits.

5. Glyvrar
Situated on the eastern shore approximately 5 km inland of the entrance to the fjord. The intertidal region consisted of concrete quaysides and slipways; elsewhere the narrow rocky foreshore comprised rock outcrops and boulders. At depths greater than 2 m the sea bed was formed of gravel and sand; beyond 12 m the sea bed was of mud and silt.

6. Lambareiði
Located on the eastern side of the fjord approximately 6 km inland of the entrance. A narrow rocky foreshore sloped into the sublittoral to 2 m (10 m offshore) at which depth it became covered by gravel deposits. At greater depths (5 m–10 m; 30 m–50 m offshore), the sea bed is formed of stones wedged in mud.

7. Gotueiði
Situated on the eastern side of the fjord almost opposite site 8. The narrow rocky foreshore sloped into the sublittoral and merged at 2 m depth into an extensive area of small boulders and shingle. Below 12 m (200 m offshore) the sea floor was of mud and occasional stones.

8. Skáli
Situated almost midway along the fjord on the western side. The narrow rocky foreshore extended only to low water level. From low water level to depth of 7 m (50 m offshore) the sea bed was formed of stones wedged in mud. At greater depths the sea bed was almost entirely of mud deposits.

9. Anir
Located on the eastern side of the fjord approximately 2 km seawards of the head-end. The narrow rocky foreshore sloped into the sublittoral, and at a depth of 1 m was covered by stones in mud. This substrate extended 40 m offshore where at 10 m depth it was replaced by silt.

10. Skálabotnur
Situated on the western side of the fjord, approximately 0·5 km from the head-on. The foreshore comprised fringing rocks and boulders; elsewhere the fjord formed a shallow 0·3–0·5 m deep lagoon which contained occasional rocks and boulders wedged in sand and gravel. A small harbour-wall constructed of large boulders was also investigated. The wall sloped steeply to a depth of 6 m; between 6–8 m the sea bed was formed of shingle deposits, and below 8 m mud formed the main substrate.

11. Fjarðará estuary
The head-end of the fjord was formed of shingle deposits which were traversed by the River Fjarðará. Stones in the brackish reaches of the estuary provide a substrate for algal attachment.

Kaldbaksfjørður

12. Hvítanes
Located on the southern shore at the entrance to the fjord. The site comprised a small sheltered bay containing rocks and boulders, surrounded by sheer cliffs. The foreshore rock continued into the sublittoral. At a depth of 22 m (approximately 50 m offshore) the sea floor was bedrock with occasional boulders.

13. Sund
Located on the southern shore almost mid-way along the fjord. The narrow, steeply sloping foreshore continued into the sublittoral to a depth of 7 m; at greater depths the sea bed was of small boulders.

14. Two-thirds of the way along the fjord
The narrow, steeply sloping, foreshore rock continued into the sublittoral to a depth of 2 m. At greater depths (down to at least 17 m) the sea floor was formed of stones and boulders wedged in sand.

15. Kaldbaksbotnur
The head of the fjord consisted of a shingle beach and sand flats, traversed by a river estuary. Occasional stones and boulders were partially immersed in an extensive area of shallow, 0·3–0·5 m deep, standing water. The sublittoral was not investigated.

Hvannasund

16. Harbour by the causeway
The wide foreshore rock sloped gently into the sublittoral; the harbour and causeway were constructed of large boulders and sloped more steeply. Adjacent to the harbour wall was a lagoon containing rocks and boulders immersed in the shallow 0–1 m deep standing water. The rocks of the harbour wall shelved to a depth of 2 m below low water level. At greater depths the sea floor was of gravel sand and mud. The centre of the sound reached a maximum depth of 8 m and the bed was of sand and mud.

17. Leiti
Situated approximately midway along the eastern side of the sound and formed of a narrow rocky foreshore with a steep slope into the sublittoral; much of the foreshore was covered by dense growths of barnacles and there were occasional pools. The bedrock continued into the sublittoral to 10 m; thence downwards the sea bed was formed of gravel, shells and *Modiolus*. Extensive beds of *Modiolus* were a prominent feature at 14 m.

Sundini

18. Norðskáli; Langasandur
Sundini is a narrow channel which separates the two large central islands of the northern Faroes. A road bridge crosses the sound at its narrowest point where it is 225 m wide. A narrow rocky foreshore is present on both sides of the sound and the rock continued to 4 m depth in the shallow sublittoral. At the bridge the sound reached a maximum depth of 7 m and the sea floor was formed of bedrock with a deposit of stones and boulders. A short distance to the north of the bridge at Langasandur a depth of 20 m was reached; the sea floor consisted of stones and shells held firm in mud deposits.

5. Results

Eulittoral vegetation

Band-forming species

Table 1 indicates the principal band forming species of the eulittoral and the littoral fringe at 13 of the 17 sites investigated. Although *Prasiola stipitata** was recorded from 5 sites it occurred as a recognizable band only at Kumlavik (site 2). *Blidingia minima* was found in both fjords and sounds and occurred throughout Skálafjørður. At several sites *B. minima* formed a distinct band of vegetation near high tide level. *Enteromorpha intestinalis* was also present at most sites, but only formed a distinct band of vegetation on the narrow foreshore at Sund (Kaldbaksfjørður, site 13). *Porphyra umbilicalis* was found everywhere except at the head-ends of Skálafjørður and Kaldbaksfjørður, where there was little firm substrate available for colonization. At six of the sites *P. umbilicalis* occurred as a distinct band. At site 14 (Kaldbaksfjørður) much of the narrow intertidal was colonized by *P. umbilicalis*.

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* Algal nomenclature follows Irvine (1982).

Table 1 Principal eulittoral band-forming species.

Species/Site	1	2	4	5	6	10	11	12	13	14	15	16	17
Blidingia minima	x	x	X	X	x	X				x		x	X
Cladophora sericea	x	x		x									x
Enteromorpha intestinalis	x	x	x	x		x	x		X		x	x	x
Prasiola stipitata	x	X		x								x	x
Spongomorpha arcta	x	x									x		x
Ulva lactuca		x	x	x	x	x	x			X		x	x
Ulothrix/*Urospora* sp.	x									x		x	
Alaria esculenta	x	x	x					X	x			x	x
Ascophyllum nodosum		X	X		X	x	x	X				x	
Dictyosiphon foeniculaceus			x			x				X	x	x	
Eudesme virescens				x						x	x		
Fucus distichus anceps								x					
F. distichus edentatus		X	x	X	X	X	x			x	X		
F. spiralis	x	X	X	X	X	X					X	x	
F. vesiculosus	x	x	X	X		x					x		
Himanthalia elongata	x	x	x	x				x					
Laminaria digitata		X	x	X	X	X			x		x	x	
L. saccharina			x			x				X	x		
Pelvetia canaliculata					x						X		
Palmaria palmata	x	x		x					X		X		
Porphyra umbilicalis	x	X	x	x	x	x		x	X	X	X		

X = Band-forming; x = present.

In most fjords fucoids were an obvious component of the vegetation. The least common of these plants was *Pelvetia canaliculata*, detected at only two sites and present as a distinct band only at Hvannasund. *Fucus spiralis* was widespread in Skálafjørður and Hvannasund but was not found in Kaldbaksfjørður. This species formed a distinct band on rocks just below high tide level. *F. vesiculosus* was less abundant than *F. spiralis*, and occurred as a distinct band at middle shore levels only at two sites in Skálafjørður. *Ascophyllum nodosum* often grew together with *F. vesiculosus* and formed a distinct band at four sites; it was not detected in Kaldbaksfjørður. *F. distichus* subsp. *anceps* was only found on exposed rock faces at Hvítanes (site 12), at the entrance to Kaldbaksfjørður. *F. distichus* subsp. *edentatus* was widespread at lower shore levels in Skálafjørður, Hvannasund, and Sundini, where it formed a distinct band. In Kaldbaksfjørður a few plants grew on rocks and stones in shallow standing water at the head-end (site 15). At Sund (site 13), and on the harbour wall at Hvannasund (site 16), *Palmaria palmata* formed a band on rocks near low water level. This species was not detected in the inner regions of Skálafjørður and Kaldbaksfjørður.

Himanthalia elongata was an obvious component of the vegetation on wave-washed lower shores at the entrances to the fjords; in Skálafjørður the species was also found at a relatively sheltered locality, Glyvrar (site 4), approximately 4 km inland of the entrance to the fjord.

Subflora (turf-forming) associations

Table 2 lists the subflora or turf-forming species recorded during the survey. As *Fucus* was largely absent from sites in more exposed situations at the entrances to the fjords, the main algal vegetation comprised small turf-forming species which often grew on a dense cover of barnacles. Species such as *Callithamnion sepositum, Ceramium shuttleworthianum,* and *Gigartina stellata* were present as small tufts or as turf-like growths. A more detailed account of the algal vegetation of open sea conditions is presented in the following paper of this series (Price & Farnham, 1982).

At less exposed sites a subflora of small species such as *Ceramium diaphanum, Enteromorpha intestinalis, Gigartina stellata,* and *Ulva lactuca* grew beneath the cover of large brown algae. At Skálabotnur (site 10, near the head-end of Skálafjørður) the underflora solely comprised small plants of *Ulva lactuca.*

In Kaldbaksfjørður, where fucoids were largely absent, the main vegetation of the eulittoral level comprised bands of *Blidingia minima, Enteromorpha intestinalis, Porphyra umbilicalis,* and *Palmaria palmata.*

Lower littoral and sublittoral fringe vegetation

The algae recorded in the lower eulittoral and sublittoral fringe levels are presented in Table 3. Species are listed separately for sites recorded in Skálafjørður and Kaldbaksfjørður. The vegetation at these shore levels was richer in species than that of the middle and upper eulittoral levels. Thirteen species were recorded only from sites in the outer areas of Skálafjørður (sites 1–5); a further 13 species occurred throughout the fjord. Red algae such as *Corallina officinalis, Ceramium rubrum, Dumontia contorta, Gigartina stellata, Polysiphonia brodiaei* and *Rhodomela confervoides,* together with a few brown algae, such as *Pilayella littoralis* and *Scytosiphon lomentaria,* were the most obvious components of the turf-forming vegetation at the more exposed entrance sites in Skálafjørður. At Hvítanes (site 12, Kaldbaksfjørður) these and other red algae such as *Cryptopleura ramosa* were recorded from lower shore pools.

In the middle and inner regions of Skálafjørður, and also at a few locally sheltered situations in the outer fjord, brown algae such as *Chorda filum, Dictyosiphon foeniculaceus, Eudesme virescens, Myrionema strangulans* (epiphytic on *Ulva lactuca*), *Pilayella littoralis, Punctaria plantaginea* and *Scytosiphon lomentaria*, together with bleached plants of *Ceramium rubrum* and *Cystoclonium purpureum* (red algae), were the most obvious components of the lower shore vegetation. A similar species assemblage was detected in the middle regions of Kaldbaksfjørður and in a sheltered lagoon near the head of Hvannasund.

Our observations showed that very few algae were restricted to the inner regions of the fjords; *Enteromorpha* spp. were more common in these regions, although filiform and filamentous brown algae were the most obvious components of the vegetation; there were very few red algae. Near the head of Hvannasund, by contrast, red algae were the most obvious component of the lower eulittoral and shallow sublittoral vegetation.

Himanthalia elongata

H. elongata occurred at lower shore levels at sites 1, 2, and 4 in the outer regions of Skálafjørður. The species was particularly common where the shores were regularly washed by waves and swell. *H. elongata* was not found in the middle and inner regions of Skálafjørður. The species was also common on wave washed shores at Hvítanes (site 12) at the entrance to Kaldbaksfjørður, but was not found at site 13 where conditions were more sheltered. *H. elongata* was not found at sites 16 and 17 in Hvannasund, although it was particularly common on the wave-washed foreshore at Viðareiði at the entrance to the sound.

Alaria esculenta

A. esculenta was an obvious component of the vegetation at the entrance to Skálafjørður, where the species was widespread on rocks in both shallow sublittoral levels and deep pools. In contrast to *Himanthalia elongata, Alaria esculenta* was also found at sites located in the middle, sheltered, reaches of Skálafjørður. Its limit of distribution along Skálafjørður was found to be just to the west of Søldafjørður, 10 km into the fjord from site 1 at the entrance. At the former location

Table 2 Principal subflora species.

Site 1 Nes Little fucoid cover Barnacles *Ceramium shuttleworthianum* *Cladophora sericea* *Corallina officinalis* *Gigartina stellata* *Phymatolithon lenormandii*	Site 12 Hvítanes *Fucus distichus anceps* Barnacles *Callithamnion sepositum* *C. hookeri* *Ceramium shuttleworthianum*	Site 17 Leiti No fucoid cover Barnacles *Ceramium shuttleworthianum*	Site 5 Strendur No fucoid cover Barnacles *Ceramium shuttleworthianum*
Site 2 Kumlavik Fucoid cover *Cladophora rupestris* *C. sericea* *Corallina officinalis* *Dumontia contorta* *Enteromorpha intestinalis* *Gigartina stellata* *Palmaria palmata* *Phymatolithon lenormandii* *Spongomorpha arcta* *Ulva lactuca*	Site 5 Strendur Fucoid cover *Ceramium rubrum* *Dumontia contorta* *Entermorpha intestinalis* *Ulva lactuca*	Site 4 Glyvrar Fucoid cover *Ceramium rubrum* *Cladophora sericea* *C. rupestris* *Cystoclonium purpureum* *Dumontia contorta* *Enteromorpha intestinalis* *Gigartina stellata* *Ulva lactuca*	Site 8 Gøtueiði Fucoid cover *Ceramium rubrum* *Chaetomorpha capillaris* *Cladophora rupestris* *Dumontia contorta* *Gigartina stellata*
Site 10 Skálabotnur Fucoid cover *Ulva lactuca*	Site 11 Hvannasund Fucoid cover *Ceramium rubrum* *Cladophora rupestris* *Dumontia contorta* *Gigartina stellata*		
Site 13 Sund No fucoid cover No subflora beneath a dense cover of: *Enteromorpha intestinalis* *Palmaria palmata* *Porphyra umbilicalis*	Site 14 No fucoid cover No subflora beneath a dense cover of: *Blidingia minima* *Porphyra umbilicalis*		

Table 3 Occurrence and distribution of lower littoral and sublittoral fringe species in A. Skálafjørður and B. Kaldbaksfjørður.

Table 3A

OUTER SITES

Alaria esculenta 1, 2, 4, 5
Chaetomorpha melagonium 2
Chordaria flagelliformis 1, 2, 4
Cladophora sericea 2
Corallina officinalis 1, 2, 4, 5
Ectocarpus fasciculatus 1, 5
Elachista scutulata 2
Himanthalia elongata 2, 5
Palmaria palmata 1, 5
Petalonia fascia 1, 2
Polysiphonia brodiaei 1, 2
Porphyra leucosticta 1, 2
Spongomorpha aeruginosa 2, 4
S. arcta 1, 2, 5

THROUGHOUT FJORD
MIDDLE FJORD SITES

‹›*Ceramium rubrum* 1, 2, 5, 7, 9
Chaetomorpha capillaris 8
›*Chondrus crispus* 8, 9, 10
‹›*Chorda filum* 2, 7, 8, 9, 10
‹›*Cladophora rupestris* 2, 5, 7, 8
‹›*Cystoclonium purpureum* 2, 8, 9
‹›*Dictyosiphon foeniculaceus* 1, 2, 4, 5, 8, 10
‹›*Dumontia contorta* 1, 3, 7, 8, 9, 10
Enteromorpha intestinalis 7, 9
Erythrotrichia carnea 7
Eudesme virescens 4, 8
‹›*Gigartina stellata* 1, 5, 8, 9
‹›*Laminaria digitata* 2, 5, 8, 9, 10
‹ *L. saccharina* 2, 4, 5, 8
Membranoptera alata 4, 8
‹›*Myrionema strangulans* 2
›*Phymatolithon lenormandii* 4, 10
‹›*Pilayella littoralis* 1, 5, 7
Plocamium cartilagineum 8
‹›*Polysiphonia nigrescens* 2, 9
P. urceolata
Punctaria plantaginea 4
Rhizoclonium riparium 7
‹›*Rhodomela lycopodioides* 2, 4, 9
‹›*Ulva lactuca* 2, 5, 9, 10

INNER SITES

Enteromorpha linza 10
Hildenbrandia rubra 10
Porphyra purpurea 9
Ralfsia clavata 10
Ulonema rhizophora 9

Table 3B Kaldbaksfjørður

OUTER SITES

Alaria esculenta
Callithamnion sepositum
Ceramium rubrum
Corallina officinalis
Cryptopleura ramosa
Delesseria sanguinea
Dermatolithon spp.
Gigartina stellata
Himanthalia elongata
Plocamium cartilagineum
Polysiphonia brodiaei

THROUGHOUT FJORD
MIDDLE FJORD SITES

Chorda filum
Dictyosiphon foeniculaceus
Ectocarpus siliculosus
Eudesme virescens
Laminaria saccharina
Myrionema strangulans
Myriotrichia clavaeformis
Palmaria palmata
Scytosiphon lomentaria
Ulva lactuca

INNER SITES

Chondrus crispus
Enteromorpha intestinalis
Pilayella littoralis

‹ = occurs also at outer sites
› = occurs also at inner sites

occasional small *Alaria* plants (less than 0·5 m in length) were detected among *Laminaria digitata* and the other small brown algae. In Kaldbaksfjørður *Alaria esculenta* grew abundantly at Hvítanes (site 12), an exposed site at the entrance to the fjord, and was also found at Sund (site 13), 5 km further in than Hvítanes. *Alaria* occurred throughout Hvannasund, even in the most sheltered areas by the causeway (site 16), where it grew among *Laminaria digitata* and *L. saccharina*. At site 17, mid-way along Hvannasund, the species formed a discontinuous band of vegetation on rocks near low water level. At several sheltered locations *Alaria esculenta* was found growing side by side with *Ascophyllum nodosum*!

Sublittoral vegetation

Occurrence and distribution of Laminaria spp.

The horizontal and vertical distributions of *Laminaria* spp. at three sites in Skálafjørður and Kaldbaksfjørður are illustrated schematically in Figs 2, 3, and 4. The type of substrate present at each site, and recorded depths, are also shown.

Laminaria digitata

L. digitata occurred throughout Skálafjørður as a narrow band in the sublittoral fringe and shallow sublittoral (cf. Fig. 3). It was not detected, although sought, on the exposed sea shore at Nes (site 1). At Skáli (site 7) the species was probably overlooked; at Skálabotnur (site 10) only small plants less than 1 m in length were detected. In Kaldbaksfjørður *L. digitata* grew in the shallow sublittoral at sites 11 and 12, but not at site 13. The species occurred throughout Hvannasund.

Laminaria hyperborea

At Nes (site 1, entrance to Skálafjørður, Fig. 2) large *L. hyperborea* plants were the dominant vegetation in the sublittoral and grew attached to the rocks and boulders to a depth of 10 m. The largest plants measured 2 m in length (stipe approx. 1 m; blade approx. 1 m) and grew at depths between 6–8 m. Below 10 m occasional *L. hyperborea* were detected on the few stones and boulders lying on the gravel sea floor. No *L. hyperborea* was found below a depth of 14 m, where the sea floor was entirely of small stones and gravel. Dense stands of *L. hyperborea* were also observed on bedrock and boulders at Raktangi headland, and at Stórafles, which lie seawards of the sites investigated in Skálafjørður.

Unlike *L. digitata, L. hyperborea* was not found in the inner reaches of Skálafjørður between Gøtueiði (site 8) and the Fjarðará estuary (site 11); it occurred at all other sites except Skáli (site 7). At Kumlavik and Saltnes (sites 2 and 3) in the outer fjord, *L. hyperborea* occurred sporadically in the shallow sublittoral to a depth of 4 m. At these depths and below only one or two small plants were sampled from one square metre.

At sites 4, 5, and 6 in Skálafjørður (Fig. 3) *L. hyperborea* was present as a narrow band of vegetation in the shallow sublittoral below the band of *L. digitata* and was not found at depths greater than 3 m. At Lambareiði (site 6) plants measured approximately 1 m long but at Glyvrar (site 4) occasional plants with short stipes and wide blades were detected. At its inner limit of distribution in Skálafjørður, site 8, occasional *L. hyperborea* grew among *L. faeroensis** in the shallow sublittoral at depths between 1–3 m.

L. hyperborea was present at all sublittoral sites investigated in Kaldbaksfjørður, Hvannasund, and Sundini. At Hvítanes (site 12) the bedrock supported a dense stand of *L. hyperborea* at depths between 1–9 m. The maximum growth of *L. hyperborea* at this site occurred at a depth of 4 m where there were many large plants with stipes 1·5 m long; *L. hyperborea* was not found at depths below 13 m. At Sund (site 13) the species formed a band of vegetation between 4 m and 10 m below low water level; between 10 m and 15 m *L. hyperborea* grew together with *L. saccharina,* while plants collected at 15 m had short stipes and very broad laminae. This form of *L. hyperborea* was also detected at site 14, a more sheltered locality in the inner region of Kaldbaksfjørður, where it grew among *L. faeroensis* and *L. saccharina* on a substrate of small

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*For comments on the current taxonomic status of *L. faeroensis* Børg. see Kain (1976). For convenience we have used this name.

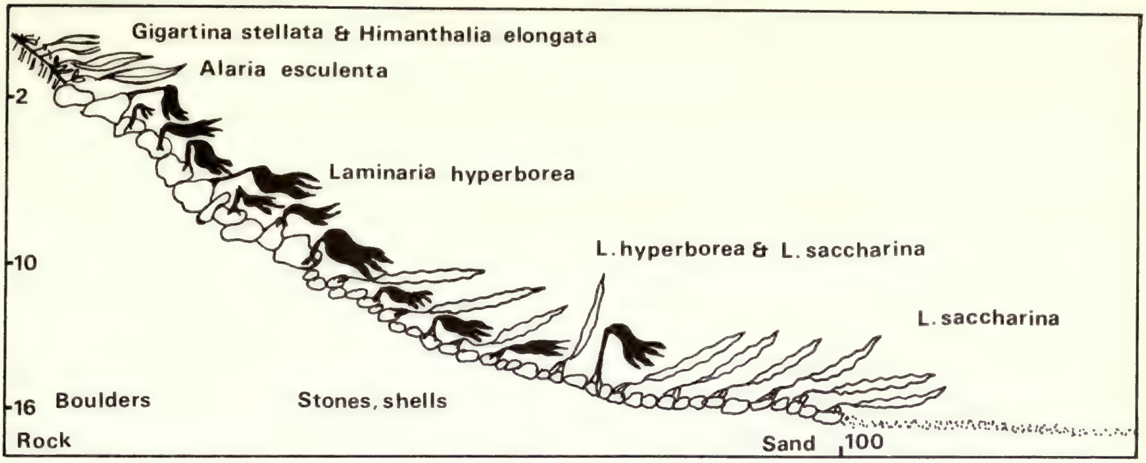
Gigartina stellata & Himanthalia elongata
Alaria esculenta
Laminaria hyperborea
L. hyperborea & L. saccharina
L. saccharina
2
10
16
Boulders
Stones, shells
Rock
Sand
100

Fig. 2 Site 1: schematic representation of vegetation and transect profile; numbers on vertical axis indicate depth in metres, and on the horizontal axis indicate distance offshore.

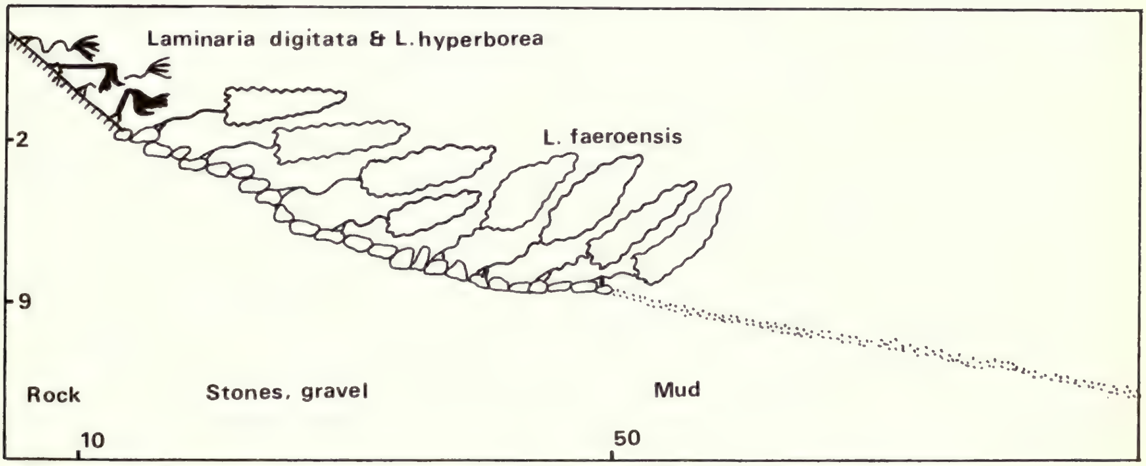
Laminaria digitata & L. hyperborea
L. faeroensis
2
9
Rock
Stones, gravel
Mud
10
50

Fig. 3 Site 6: schematic representation of vegetation and transect profile; details as for Fig. 2.

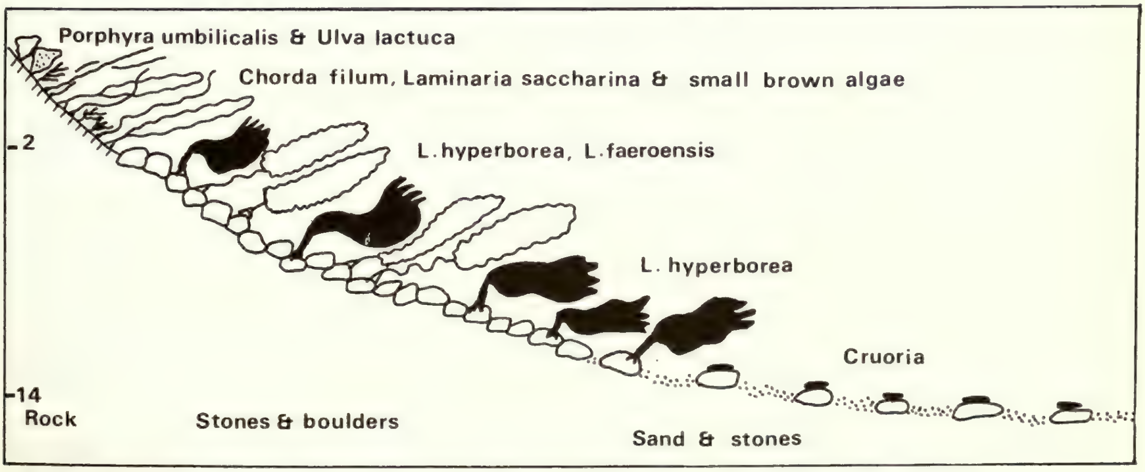
Porphyra umbilicalis & Ulva lactuca
Chorda filum, Laminaria saccharina & small brown algae
L. hyperborea, L. faeroensis
L. hyperborea
Cruoria
2
14
Rock
Stones & boulders
Sand & stones

Fig. 4 Site 14: schematic representation of vegetation and transect profile; details as for Fig. 2.

boulders and stones (Fig. 4). A dense band of *L. hyperborea* occurred in the shallow sublittoral (2–4 m depth) at site 17 in Hvannasund. At greater depths the species grew together with *L. saccharina*; at 10–14 m the sea floor was covered with extensive *Modiolus* beds and these were widely colonized by *L. hyperborea*. At the head of Hvannasund (site 16) the form of *L. hyperborea* with broad fronds colonized stones and shells at depths between 4–8 m. Typical forms of the plant grew on the rocks and boulders of the harbour and causeway in the shallow sublittoral (2 m depth).

Laminaria saccharina

The typical form of *L. saccharina* was found at most sites in Skálafjørður, but was noticeably absent from sites 9 and 10 near the head of the fjord. *L. saccharina* grew among *L. digitata* and *L. hyperborea* in the shallow sublittoral regions (between 0–2 m). At sites 4 and 5 the species formed a narrow band of vegetation at slightly greater depths (3–4 m) between an upper band of *L. hyperborea* and a lower, extensive, area of *L. faeroensis*. At Nes (site 1, Fig. 2) *L. saccharina* and *L. hyperborea* formed a mixed community of plants inhabiting the boulder and gravel sea floor at depths between 10–14 m. *L. saccharina* grew on small stones, or even unattached, at depths between 14–16 m (approximately 100 m offshore); it did not grow on the muddy sea floor below 16 m.

In Kaldbaksfjørður the species grew together with *L. digitata* and *L. hyperborea* in the shallow sublittoral (0–2 m). At Hvítanes (site 12) *L. saccharina* was present at greater depths (10 m and below) in open stands of *L. hyperborea*; mixed stands of the two laminarians were also seen at site 13 at depths between 2–8 m. At greater depths *L. saccharina* developed wider blades and longer stipes, and was not easily distinguishable from *L. faeroensis*. The typical form of *L. saccharina* was only found in shallow waters at the sheltered site 14 in Kaldbaksfjørður. It was found among *L. digitata* and *L. hyperborea* in both shallow and deep sublittoral regions in Hvannasund (sites 16 and 17). At site 16 (head end) plants with long stipes and broad laminae formed a mixed community with the broad form of *L. hyperborea*.

Laminaria faeroensis

The *L. faeroensis* form of *L. saccharina* occurred widely in the sheltered regions of fjords. In Skálafjørður this species was absent from the outer sites (1, 2, and 3), but was present everywhere else on unstable substrates in the deeper sublittoral (Fig. 3). At Glyvrar (site 5), for example, *L. faeroensis* not only colonized small stones on the muddy sea floor, but in some places appeared to be unattached. *L. faeroensis* was the dominant species between 4–12 m (approximately 100 m offshore). Plants were often large in size, and one specimen plant measured 2·7 m in length (stipe 1·2 m; lamina 1·5 m long, 0·6 m wide). At Gøtueiði (site 8) beds of *L. faeroensis* spread to a distance of 200 m offshore.

At sites 13 and 14 in Kaldbaksfjørður, it was difficult to distinguish *L. saccharina* from *L. faeroensis*; most *L. saccharina* had wide laminae and long, but solid, stipes. *L. faeroensis* was not detected in Hvannasund, but was widespread in Sundini.

Subflora vegetation

Three associations of algae were recognized in the subflora vegetation in Skálafjorður, Kaldbaksfjørður, and Hvannasund. The constituent species of the subflora vegetation are listed in Table 2 and the sites at which they were recorded is given.

An association, mainly of red algae such as *Audouinella purpurea, Callophyllis (Euthora) cristata, Chaetomorpha melagonium, Epilithon membranaceum, Membranoptera alata, Palmaria palmata, Phycodrys rubens, Polysiphonia urceolata, Ptilota plumosa, P. serrata* and the *Aglaozonia* stage of *Cutleria multifida* was detected on the stipes of *Laminaria hyperborea* and on adjacent rocks and boulders. At most sites the number of species present decreased with increasing depth. This association occurred in the outer regions of fjords where *L. hyperborea* was more abundant; an impoverished form of the association, containing many fewer red algae, was detected at Lambareiði (site 6) in the middle regions of Skálafjørður.

A distinct association of plants was recorded on or among *Laminaria saccharina* on unstable substrates in the outer fjord or on/among *L. faeroensis* in the middle and inner regions.

Ceramium rubrum, Chorda filum, Desmarestia aculeata, D. viridis, and *Ulva lactuca* colonized stones and boulders within the stand of *L. saccharina,* while small brown algae such as *Ectocarpus fasciculatus* and *Litosiphon filiformis* were common epiphytes on the laminae of *L. saccharina.*

The crustose species *Cruoria pellita, Lithothamnium glaciale,* and *Pseudolithoderma extensum* were detected as a distinct association on rocks and boulders in deeper waters at the entrance to Skálafjorður, and occurred sporadically in the middle and inner regions, where solid substrates were available (Fig. 4).

Several species were found only at the inner end of Skálafjørður (sites 9 and 10); these included *Asperococcus turneri, Erythrotrichia carnea, Polysiphonia elongata, Sphacelaria plumosa,* and the *Trailliella* phase of *Bonnemaisonia hamifera.* Several of these algae were growing on plastic bristle-like debris strewn over the sea floor. *Antithamnion floccosum* and *Sphacelaria rigidula* were also found on this substrate..

At most sites in Skálafjørður and Kaldbaksfjørður, subflora was sparse beneath the canopy of *Laminaria faeroensis.*

In Hvannasund, by contrast, a subflora rich in both numbers of species and individual luxuriances was detected in the deeper sublittoral zone. Several species occurred here which were not recorded in Skálafjørður and Kaldbaksfjørður; these included *Callocolax neglectus* parasitic on *Callophyllis laciniata, Fimbrifolium dichotomum, Lomentaria clavellosa, Phyllophora truncata,* and *Polyides rotundus.* Unusual growth forms of several red algae were detected at the head end of Hvannasund (site 16). A crisp, more branched, form of *Odonthalia dentata* was common in the deep sublittoral, together with a narrow and more branched form of *Callophyllis cristata* and the *lingulata* form of *Phycodrys rubens.*

Site 18. Sundini

The Streymoy shore of Sundini near the road bridge was mainly of sand and gravel deposits uncolonized by algae; boulders standing in fast-flowing water supported large growths of *Porphyra umbilicalis.* Near high tide level the gravel beach was colonized by maritime flowering plants, and *Vaucheria coronata* was found on damp soil surrounding the plants. The narrow foreshore on the Eysturoy side of the sound carried a dense cover of fucoids; filiform and filamentous brown and green algae were detected in lower shore pools.

Alaria esculenta and *Laminaria hyperborea* formed a distinct but narrow band of vegetation on bedrock in the shallow sublittoral. *L. faeroensis* grew attached to stones and boulders at depths between 2–5 m. Although *Desmarestia aculeata* grew among the *L. faeroensis,* almost no other subflora was found associated with the cover of the latter. Stones and boulders at depths below the *L. faeroensis* level were colonized by crustose algae such as *Lithothamnium glaciale* and *Pseudolithoderma extensum.*

At Langasandur (2 km north of the road bridge) most of the narrow intertidal was covered by dense growths of *Ascophyllum nodosum.* A narrow band of *Laminaria digitata* was present in the shallow sublittoral, and the broad form of *L. hyperborea* grew on bedrock at depths between 1–4 m; a few epiphytes colonized the stipes of *L. hyperborea.* At greater depths (4–10 m) *L. faeroensis* was detected growing on a deposit of stones and boulders covering the sea floor; *Desmarestia aculeata* was occasionally present. *Phycodrys rubens, Polysiphonia elongata,* and crustose species formed an open community of plants and stones and shells between 10–18 m. No vegetation was detected below a depth of 20 m.

6. Discussion

Comparison with Børgesen's observations

Our observations on the algae of the littoral fringe differ little from those made by Børgesen (1905), who described an upper eulittoral 'formation of Chlorophyceae' which was composed of three bands of vegetation. The predominant species present in these bands were *Prasiola stipitata, Blidingia minima* and *Enteromorpha intestinalis.*

Børgesen also described a 'Fucaceae formation', which comprised five bands of algae; these were *Pelvetia canaliculata, Fucus spiralis, F. vesiculosus, Ascophyllum nodosum* and *F. distichus* subsp. *edentatus*. We detected these bands of algae and also noticed that these fucoids were absent from exposed sites at the entrances to the fjords; there, *F. distichus* subsp. *anceps* was the dominant fucoid. Fucoids were recorded throughout Skálafjørður, and were particularly abundant at sites where a firm substrate prevailed; in Kaldbaksfjørður these algae were conspicuously absent from the inner regions where littoral rocks were colonized by dense growths of *Enteromorpha intestinalis, Palmaria palmata*, and *Porphyra umbilicalis*. The natural foreshore in this area has recently been covered by a steeply sloping boulder foreshore which supports a new road. Although *A. nodosum* was widespread in the sheltered parts of Skálafjørður, it was also found in sheltered locations at very exposed sites. At both Hvítanes (site 12) and Kumlavik (site 2) the species grew together with *Alaria esculenta*.

A subflora or turf-forming vegetation was detected at most sites; in exposed situations *Callithamnion sepositum, C. hookeri, Ceramium shuttleworthianum, Corallina officinalis*, and *Gigartina stellata* were particularly abundant; *C. sepositum* and *C. shuttleworthianum* did not occur in sheltered areas and the other species were less common. In the sheltered regions of Skálafjørður and Kaldbaksfjorður species of red algae were a less obvious component of the vegetation of the eulittoral level, and at Skálabotnur (site 10) there were no red algae beneath the cover of *Fucus* spp. Børgesen (1905) described a thick turf of *Corallina officinalis* from lower shore levels at exposed sites; he commented that this vegetation is replaced in sheltered areas by prolific growths of filamentous and filiform brown algae which he named a '*Stictyosiphon* association'. Our observations revealed that this type of vegetation was widespread in the inner regions of Skálafjørður, Kaldbaksfjørður and in a sheltered lagoon near the head end of Hvannasund. Both Børgesen's and our surveys recorded a few red algae (*Ceramium rubrum, Cystoclonium purpureum, Dumontia contorta*, and *Rhodomela lycopodioides* among the vegetation of filiform brown algae.

We detected *Devaleraea* (*Halosaccion*) *ramentacea* at the head end of Hvannasund where it grew in shallow standing water in pure stands; Børgesen found the species in similar conditions near Klaksvik.

Although we noted more green algae, particularly *Enteromorpha* spp., in the shallow sublittoral regions at the head ends of Skálafjørður and Kaldbaksfjørður, we did not locate the large growths of *Monostroma fuscum* noted by Børgesen as characterizing a '*Monostroma-Enteromorpha* Association'. Børgesen indicated that this association occurred in shallow water at the heads of fjords with considerable inflow of freshwater, and considered it to be perennial. We too detected the loose-lying mats of *Ceramium rubrum, Chorda filum, Enteromorpha* spp., *Rhizoclonium riparium*, and *Scytosiphon lomentaria* in very shallow water at the head end of Skálafjørður, and additionally found *Capsosiphon fulvescens*, growing in shallow, brackish water in the estuaries at the heads of Skálafjørður and Kaldbaksfjørður.

Børgesen (1902) remarked that *Alaria esculenta* was widespread in the Faroes and, that while it showed a preference for open sea shores, it may also occur in the more sheltered interior of a fjord; our observations of some *Alaria* plants growing side by side with *Ascophyllum* confirms this and supports Russell's (1978) comments that 'abundance measures are a more reliable indicator of environmental conditions than presence data . . .'. We were unable to locate *A. pylaii* which Børgesen (1905) recorded from sheltered waters in Skálafjørður.

Børgesen (1905) described the '*Halidrys* Association' from the shallow infralittoral region at Glyvrar in Skálafjørður; apparently this was the only site from which the species was known in the Faroes. *H. siliquosa* grew among *Laminaria* spp. and supported a number of brown algal epiphytes such as *Punctaria latifolia*. We failed to find *Halidrys* at Glyvrar despite an intensive search.

Laminaria spp. are the most obvious component of the vegetation of the sublittoral region in the fjords and sounds. Børgesen (1905) described a 'Laminariaceae Association' which he noted as being widespread in the Faroes. The occurrence and distribution of *Laminaria* follows the patterns described by Børgesen (1905) and other workers (Kain, 1960; Norton & Milburn, 1972). *Laminaria hyperborea* was the dominant species on firm substrates where more exposed conditions prevailed. In the sheltered parts of Skálafjørður and Kaldbaksfjørður it occurred as a narrow band in the shallow sublittoral but was absent from the innermost regions; a broad form of the species which resembled the *cucullata* form of *L. digitata* was found in deeper waters in the sheltered parts of fjords.

The *Laminaria faeroensis* form of *L. saccharina* occurred abundantly in Skálafjørður and Kaldbaksfjørður. Our observations parallel those of Børgesen who recorded *Laminaria* with large laminae and long, hollow stipes from the deeper parts of fjords. Although the species was common in the sheltered parts of Sundini, it also occurred near the narrows where there was a strong current.

The normal form of *Laminaria saccharina* grew in situations where there was more water movement. At most of the sites investigated the species grew in the shallow sublittoral levels among *L. digitata* and *L. hyperborea*; it was also widespread on unstable substrates in deeper waters at the entrance to Skálafjørður. We confirmed Børgesen's observations that in certain situations it was difficult to distinguish between *L. saccharina* and *L. faeroensis*.

We detected *Desmarestia aculeata* and *D. viridis* growing among *L. faeroensis* on unstable substrates in deeper waters; the epiphyte *Porphyropsis coccinea* was also found. Børgesen described a '*Desmarestia* Association' which appeared to comprise almost pure stands of *Desmarestia* spp. from similar habitats.

We failed to find eel-grass *Zostera marina* in sheltered habitats. Børgesen commented that the plant was rare on the Faroes and cited only one locality (Vaag fjord) for this community. The leaves of *Zostera* bore a number of small algal epiphytes.

A well developed subflora was detected at the entrances to Skálafjørður and Kaldbaksfjørður and throughout Hvannasund. The subflora consisted mainly of red algae growing either as epiphytes on the stipes and holdfasts of *Laminaria hyperborea* or on firm substrate between *L. hyperborea* plants. This subflora vegetation differs little from the vegetation described by Børgesen as a '*Laminaria hyperborea* Association'. This assemblage of species was not found in the inner regions of fjords because either *L. hyperborea* was absent or suitable substrate was not available. Almost no subflora was detected beneath the cover of *L. faeroensis,* which appears to form a blanket covering over large areas of the sublittoral in Skálafjørður and Kaldbaksfjørður. In contrast, a well developed subflora was found throughout Hvannasund; this vegetation was recorded both among *Laminaria* spp. and from levels below the lower limits of *Laminaria.* Species were detected which were not listed by Børgesen under his '*Laminaria hyperborea* Association' but included by him in a 'sublittoral Floridae formation', which usually occurred in open sea conditions rather than in sheltered waters; the formation is characterized by such species as *Callophyllis cristata, C. laciniata, Delesseria sanguinea, Fimbrifolium (Rhodophyllis) dichotomum,* and *Phycodrys rubens.* The causeway which divides Hvannasund was constructed in the middle 1970s. The main effect of this was the elimination of water current through the narrows between Borðoy and Viðoy and the creation of still water conditions; vegetation nevertheless retains many of its open water characteristics (such as the abundance of red algae and the presence of species such as *Alaria esculenta*) although sheltered conditions are suggested by the occurrence there of the broad form of *Laminaria hyperborea.* It was hoped that the investigation of the narrows between Streymoy and Borðoy would reveal a similar type of vegetation. At Nordskáli, near the road bridge, *Alaria esculenta* and *Laminaria faeroensis* were found but the impoverished subflora did not resemble the vegetation in Hvannasund.

Børgesen described a '*Lithoderma* Association' from deep waters in open sea situations; this association comprised a few small filamentous and frondose algae together with a number of crustose species. We detected a similar community inhabiting stone and shell substrates at the entrance to Skálafjørður but did not find the community in the inner regions of Skálafjørður. A community of crustose algae dominated by *Cruoria* sp. was present in deep waters in Kaldbaksfjørður.

Both surveys recorded *Phycodrys rubens* as the most frequent and sometimes the only macroalga in deeper waters; the species occurred in the sheltered middle regions of fjords, but was not found in the innermost regions. Plants resembling the *lingulata* form of *P. rubens* were recorded in deep waters where there was little current.

Several species which were not recorded by Børgesen (1902; 1905) were found in deeper waters at the head end of Skálafjørður; *Asperococcus turneri* was found on stones and shells lying on the muddy sea floor; the species has not been found elsewhere in the Faroes but is common in the Shetlands. The tetrasporophyte stage of *Bonnemaisonia hamifera (Trailliella)* was detected growing on plastic bristle-like debris also on the muddy sea floor. Members of the Bonnemaisoniaceae have in recent times spread throughout much of northern Europe. Irvine *et al.* (1975) first recorded *B. hamifera* (as *Trailliella*) and *Asparagopsis armata* (as *Falkenbergia*) from the Shetlands, and Printz (1952) similarly noted *Bonnemaisonia hamifera* and *B. asparagoides* from Norway. Neither *Asparagopsis armata* nor *Bonnemaisonia asparagoides* gametophytes were found on the Faroes despite intensive searching. A few other uncommon species (*Antithamnion floccosum, Polysiphonia elongata,* and *Sphacelaria rigidula*) were also recorded from this habitat and are also known from the Shetlands and Norway.

Comparison with other fjords

The algal vegetation of fjord systems in Iceland, Norway, Shetland, and Scotland has only recently attracted scientific interest. Tittley *et al.* (1977) described how Sullom Voe (a fjord-like formation on the nearby Shetlands) differed from fjord and loch formations elsewhere in Norway and Scotland. Sullom Voe is a long inlet of the sea with an almost constant salinity throughout, unlike the Hardangerfjord in Norway in which freshwater drainage from the surrounding hinterland has a direct effect on the salinity regime of the fjord. Similar types of reduced salinity regimes were described by Munda (1972, 1978*a*, 1978*b*) for fjords on Iceland. River estuaries drain in the head ends of Skálafjørður and Kaldbaksfjørður, and, according to Børgesen (1905), the freshwater inflow can bring about a local depression in salinity. Our observations indicated that in July 1980 there was no appreciable reduction in salinity at the heads of Skálafjørður and Kaldbaksfjørður. Hvannasund resembled Sullom Voe in that it was a narrow inlet of the sea without any significant inflow of freshwater at the head.

A comparison of the sublittoral vegetation of Sullom Voe with that in Kaldbaksfjørður and Skálafjørður revealed a number of differences. *Laminaria hyperborea* was present as dense forests on bedrock at the entrances to Sullom Voe, Skálafjørður, and Kaldbaksfjørður, but in Sullom Voe the species was also found at the head, where it formed a narrow but distinct band in the shallow sublittoral. In both Skálafjørður and Kaldbaksfjørður, *L. hyperborea* did not grow at the landward ends. The broad ('cucullate') form of *L. hyperborea,* found in the inner regions of Kaldbaksfjørður and Hvannasund, was not detected in Sullom Voe.

Laminaria faeroensis showed a very restricted distribution in Sullom Voe and was recorded only in the most sheltered regions. In Skálafjørður and Kaldbaksfjørður, *L. faeroensis* occurred throughout save only for the entrances. Sheltered, deeper waters in Sullom Voe were populated by the normal form of *L. saccharina,* whereas in Skálafjørður and Kaldbaksfjørður the normal form of the species was only found in the shallow infralittoral levels.

Although a mainly red algal subflora was detected in both Sullom Voe and Skálafjørður, the vegetation was much less extensive in Skalafjørður and was absent from the inner regions. In both systems, a mainly brown algal subflora was associated with stands of *L. saccharina*/*L. faeroensis.* The turf-forming vegetation in the shallow sublittoral was also similar in these systems. Species such as *Phycodrys rubens, Polysiphonia elongata* and *Phyllophora crispa* were the principal components of the vegetation in deep water throughout Sullom Voe. *Phycodrys rubens* was the most frequently observed species in the deeper parts of Skálafjørður, but it did not occur in the inner regions of the fjord. *Polysiphonia elongata,* by contrast, was found only once at the inner end of Skálafjørður and *Phyllophora crispa* was not found at all in Skálafjørður. *'Trailliella'* grew on mud and silt in the deeper parts of Sullom Voe, and was found in a similar habitat in Skálafjørður.

Although some fucoids grew permanently immersed in shallow standing water at the heads of Skálafjørður and Kaldbaksfjørður, others formed a distinct and dense zone of vegetation where intertidal substrate was available; a well developed fucoid vegetation was present on rocks at the head end of Sullom Voe, but was absent in the shallow sublittoral levels. The vegetation in Hvannasund was similar to that in the inner regions of Sullom Voe in several respects: (i) there was a distinct zonation of eulittoral species on the harbour and causeway walls; (ii) a narrow but distinct band of *Laminaria hyperborea* was present in the shallow sublittoral zone; (iii) a well-developed subflora with many red algae was present in deeper waters.

In Norway and Iceland fjords are much longer, more sheltered, and receive a greater inflow of freshwater. Consequently different patterns of algal occurrence and distribution have been recorded. Jorde & Klavestad (1963) described a 'fjord effect' which involved '. . . an impoverishment of the vegetation and an abrupt rise in the lower limit of continuous vegetation of larger brown and red algae on passing from the outer fjord areas inwards . . .'. The occurrence and distribution of algae in Skálafjørður and Kaldbaksfjørður are in some respects similar to the patterns of distribution in Hardangerfjord, Norway (Jorde & Klavestad, 1963) and in Dýrafjördur, Iceland (Munda, 1972, 1978*a*, 1978*b*). Brackish water species *Capsosiphon fulvescens, Percursaria percursa*, and *Rhizoclonium riparium* were recorded from saline meadows in Hardangerfjord and from oligohaline habitats in the inner part of Dýrafjördur; *C. fulvescens* and *R. riparium* occurred in the estuaries at the heads of both Skálafjørður and Kaldbaksfjørður. On the other hand, *Fucus ceranoides* occurred in river estuaries in fjords in Norway and Iceland, but has not been found on the Faroes. An association of filamentous green and brown algae (*Chaetomorpha capillaris, Dictyosiphon* spp., *Enteromorpha* spp., *Stictyosiphon* spp., and ectocarpoids) was widespread in the inner brackish region of Hardangerfjord and Dýrafjörður; a similar association was restricted to the inner ends of Skálafjørður and Kaldbaksfjørður. *F. spiralis* and *F. vesiculosus* occurred throughout the Norwegian, Icelandic and Faroese fjord systems. In Norway, *F. serratus* was the dominant fucoid at lower shore levels, whereas on the Faroes *F. distichus* subsp. *edentatus* occupied these levels. *F. serratus* was found growing in the shallow sublittoral in the inner reaches of the Hardangerfjord, although Børgesen (1902) did not find it and dismissed previous records.

The limit of distribution of *Laminaria saccharina* in Dýrafjörður, Iceland, is salinity dependent and coincides with the 28‰ isohaline (Munda, 1978*b*). The species occurs throughout the middle and outer parts of Hardangerfjord, these remaining more or less saline throughout the year; its limit of distribution coincides with a summer salinity reduction to 15‰ (Jorde & Klavestad, 1963). *L. digitata* shows a similar salinity dependent distribution in both fjords. On the Faroes, both *L. saccharina* (incl. *L. faeroensis*) and *L. digitata* were found at the head of Skálafjørður, where presumably the salinity remains high for most of the year. In the Norwegian, Icelandic and Faroese fjordic systems, a subflora of predominantly filamentous brown algae is associated with *Laminaria saccharina/L. faeroensis,* and this community is particularly common in the sheltered inner reaches.

The occurrence of *Laminaria hyperborea* in the Dýrafjörður, Hardangerfjord, and Skálafjørður is largely restricted to the outer exposed regions where it can form dense stands. In more sheltered conditions, *L. hyperborea* occurs only as a narrow band in the shallow sublittoral levels; in Hardangerfjord, Dýrafjörður, and Skálafjørður, the inner limit of distribution of *L. hyperborea* is in a region where the salinity only very occasionally falls below that of sea water. There, and further into the fjords, *L. hyperborea* is replaced by *L. saccharina.* The broad form of *L. hyperborea* was widespread in the inner parts of Kalbaksfjørdur but has not been recorded from the Norwegian and Icelandic fjords. The subflora associated with *L. hyperborea* is also restricted to the outer regions of fjords in Norway, Iceland, and the Faroes; an impoverished subflora was, however, recorded from the middle and inner regions of Skálafjørður. A few species of red algae, such as *Ceramium rubrum* and *Polysiphonia elongata* recorded from the inner part of Skálafjørður, were also found in the inner regions of Hardangerfjord. A dense turf of *Corallina officinalis* was present in the lower littoral and sublittoral fringe levels at the entrances to fjords in Norway, Iceland, and the Faroes. In Norway and on the Faroes *Polysiphonia brodiaei* was also commonly present. In all fjordic systems this vegetation did not occur in sheltered waters, and was replaced by filamentous brown algae associated with *Dumontia contorta, Cystoclonium purpureum,* and *Rhodomela* spp.

7. Conclusions

The occurrence and distribution of marine algae are similar in Skálafjørður and in Kaldbaksfjørður; the vegetation in Hvannasund and Sundini differs considerably from these locations. In Hvannasund and Sundini species which are characteristic of both exposed and sheltered conditions were detected, although in Sundini the subflora of the eulittoral and sublittoral levels was rather impoverished. The luxuriant subflora, particularly of red algae, found in the inner parts of Hvannasund indicated that there was little or no 'fjord effect', and that Hvannasund was an inlet of the sea. The vegetation in Sullom Voe, Shetlands, similarly showed little or no 'fjord effect'.

A reduced 'fjord effect' was detected in Skálafjørður and Kaldbaksfjørður, and was indicated by the absence of *Laminaria hyperborea* and of red algae from the inner regions of these fjords. The reduced 'fjord effect' was probably brought about by the rivers which drained into the heads of these fjords. The resulting estuarine conditions were only local and in July 1980 were restricted to an area within a few hundred metres radius of the river mouth. In Dýrafjörður on Iceland by contrast the estuarine area was more extensive and the 'fjord effect' noticeable over a greater distance along the fjord. In the much larger Hardangerfjord system, which drains an extensive hinterland, the flow of freshwater into the fjord has a more pronounced effect on the occurrence and distribution of algae. Despite the less extensive 'fjord effect' in Skálafjørður and Kaldbaksfjørður than in Hardangerfjord and Dýrafjörður, the occurrence and distribution of marine algae in these systems is more closely similar to the latter fjords than to inlets of the sea such as Hvannasund and Sullom Voe.

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Seaweeds of the Faroes
3: Open shores

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Synopsis

Detailed studies on the intertidal and, more especially, the subtidal of sheltered and exposed open shores are presented. Only comparative changes, or detailed differences for particular groups or taxa, are given for the intertidal, since Børgesen's 80-year-old data were so accurately observed and well expressed. The earlier information lacked details derived from direct observation of the subtidal flora, now available for the first time. Vertical and horizontal distribution patterns of the major subtidal canopy organisms at the 44 open-shore sites examined are discussed and profiles of particularly detailed transect studies presented. Data on subordinate organisms (epiphytes; epizoic and epilithic underflora) and on flora at depths below the laminarian limits are considered, after presentation in tabular summarized form. Specialized situations (detrital, scour-tolerant species; consistent epizoic or other animal associations; the effects on distribution of lower littoral pools or standing waters) are examined. Amplification or revision of previous information by present data, and apparent comparative changes in the last 80 years, are discussed for the subtidal flora and its distribution. Particular rarities, unusual distributions, and new records are briefly considered.

1. Introduction

There is no easy and absolute distinction between fully marine macroflora distribution patterns in sheltered waters and those in the open, more wave-exposed situations. This appears true

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whatever the geographical location in temperate and cooler waters. Transitions from one set of most usual patterns to the other are gradual, or (at most distinct) step-wise. Aside from that, most shores present complex mosaics of exposed and sheltered local areas that, as with the overall impressions of shores, are clear enough in themselves until one attempts detailed analysis of the individual biotic or environmental facets, when blurring of hitherto clear-cut patterns is immediately experienced. 'Exposure' (as a concept applied to areas experiencing strong water-movement) is not limited to the effects of wave-action; swell, up-carry, scour, tide-race and so on are often as important as the direct effects of true wave-impact, are more widespread as phenomena, and can often produce similar results. This is particularly true for the much-sculpted northern and southern Atlantic oceanic islands, where sheer geographical/physiographical position of an open shore area is, as with its topography, no necessarily firm guide to its exposure/shelter characteristics.

It will therefore be appreciated that the open shores of the heavily-glaciated, volcanic Faroe Islands are by no means necessarily all of extreme exposure to strong water-movement effects, and that it is not easy to draw clear-cut limits in coverage between the floras of sheltered fjords/sounds (Tittley *et al.*, 1982) and those of the open shores. Essentially, the present paper is concerned with non-fjordic shores, although with such a complex configuration as that of the Faroese shores, even the concept of 'fjord' is not always clear. Outer parts of fjords or sounds, especially where (as in Raktangi, at the confluence of Tangafjørður and Skálafjørður, Streymoy) a wide entry has permitted the direct effects of essentially open-shore wave characteristics to impact a rock promontory *within* a fjord, show few distinctions from open shore conditions in either intertidal or the first 30 m of the subtidal. Some data from such shores are briefly included for comparison within the present coverage, although overlap between the second paper in this series and the present text has been kept to a minimum.

A general background to the work pattern has already been presented by Irvine *et al.* (1982), Irvine (1982), and Tittley *et al.* (1982). Data on certain taxa of importance on open shores have also been incorporated in papers of more specific coverage (e.g. on *Callithamnion*; Dixon & Price, 1981). General background presented here therefore concerns characteristics of open shore biota not already adequately covered elsewhere. Whatever the style of marine vegetational study in the Faroes, continual reference to the very effective work by Børgesen (1895–1902, as to visits; 1902–1905, as to publication dates) is unavoidable. Although certain changes seem to have taken place in the 80-odd years since then, the possibility of such changes being one of the major considerations behind the present work scheme, it is impressive that he was able to make such detailed and accurate descriptive accounts, as will emerge later of considerable validity still today. The dredging work then carried out gave good insight into the nature of the subtidal open shore flora and its distribution, but (from absence of direct observation) that still represents the least detailed part of his account. His descriptions of the open shore (sheltered or wave-washed) intertidals are of such widespread application and sufficiently comprehensive as to make detailed repetition unnecessary, save where there are changes or differences in detail. Points already well made in his accounts of those intertidals are therefore not further elaborated here, the present text concentrating on subtidal detail from direct observation and on critical variation from the earlier intertidal data.

The configuration of the generally rugged coastlines of the Faroes and the mosaic nature of the habitat distribution provided thereby are well summarized in Børgesen's analysis of the overall algal vegetation (1905: 705–706), reference to which is recommended for full appreciation of certain background characteristics.

A comment on terminology is appropriate. We have generally accepted the limits of vertical divisions of the shore suggested by Børgesen (1905) for the Faroes. For the purposes of the present paper, the most important shore levels requiring clear definition are those concerned with the lower intertidal, subtidal fringe, and subtidal proper. In presenting definition, we also clarify our terminology. We accept that generally speaking the lower limit of *Himanthalia* is an appropriate lower limit for what Børgesen (1905: 708–710; 733–735) referred to as his *Littoral Region*; we use the term *intertidal* to cover the same vertical amplitude, and include within that general term all those areas, including the splash or spray upper levels (often far inland) still within the sphere of marine influence such that some algae also found lower on shore in direct tidal contact will grow there (e.g. *Audouinella purpurea*). *Subtidal* is therefore applied to all levels, uncovered or not in usual tidal sequences at springs periods, below the lower limit of *Himanthalia*. Where the latter is not present in shelter, we take the upper limit of whatever laminarians are present at band-forming density as the limit between intertidal and subtidal. Across these limits usually lies the *subtidal fringe,* created by tidal movement, swell, and/or any form of variable water run that gives a variable regime of immersion/emersion to any organisms present there. The width and height on shore are locally variable, as are the detailed presences of organisms, but *Alaria* and some outliers of *Himanthalia* (or even most of the latter, where present in less wave-exposed locations) are usually involved. We have therefore employed the term *subtidal fringe* in a somewhat general sense, without definition as to rigid upper and lower limits, to indicate rather an area around the usual calm low water level of medium tides and subject to a fairly similar variation in ambient conditions. Configuration of this fringe area varies considerably between shores and is much affected by the presence of incut channels, downwash surfaces and upcarry grooves. The relationships of lower shore pools and standing waters to such a fringe area are debated later. Minor differences of concept between this treatment and Børgesen's (1905) approach are easily appreciated by reference to his earlier (1905: 708–711) comments.

2. Methods

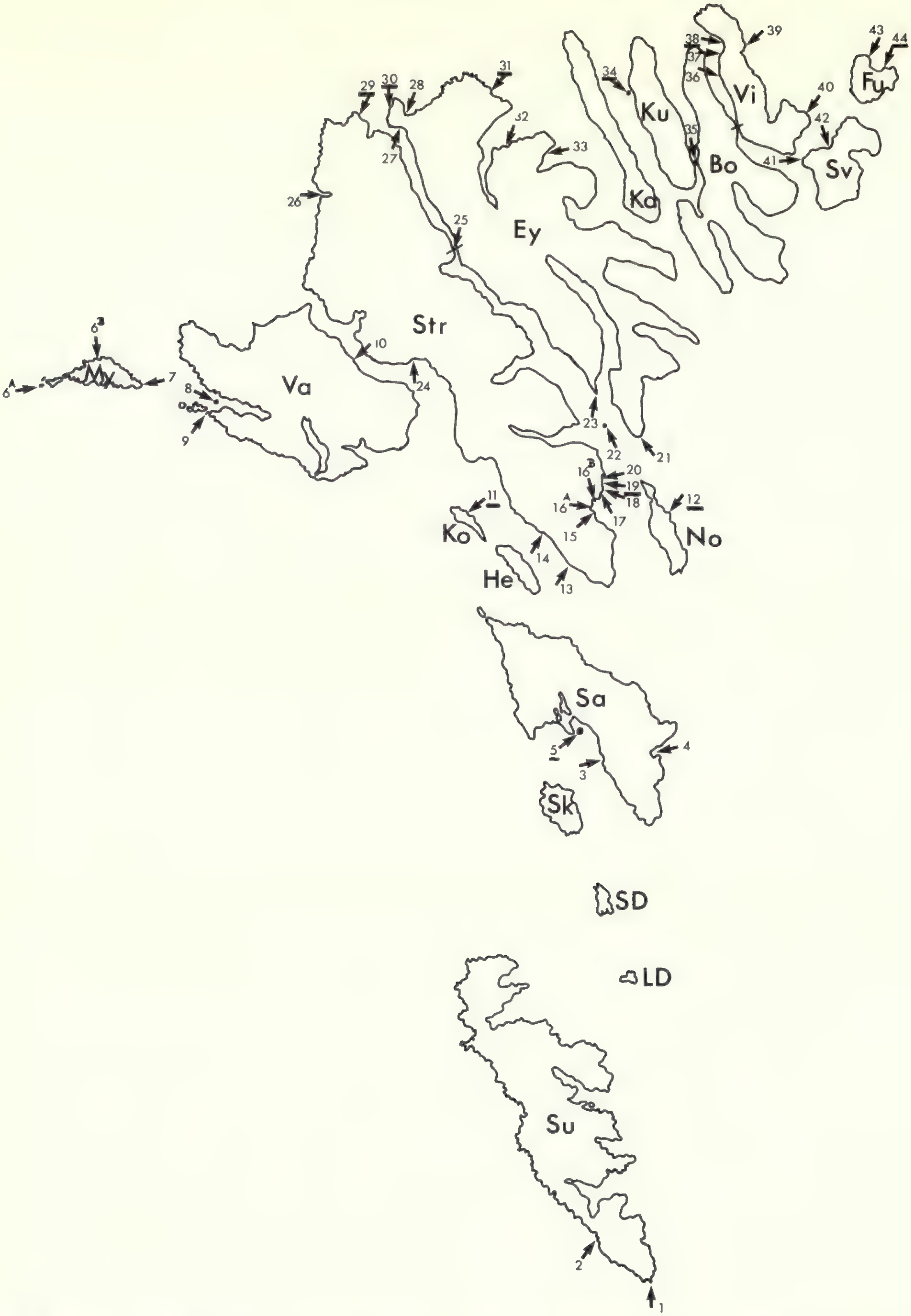
All observational data, quantitative and qualitative, were directly derived by shore examination or scuba. Profiles related to low water level were constructed from diving and intertidal notes, including depths recorded from wrist gauges or by direct measurement. Vegetational densities have been derived from counts of larger flora and from subjective estimates of smaller species. Quadrat reading was not possible, except in the case of specialist studies on particular taxa. Material of doubtful determination in the field was subsequently confirmed or revised in the laboratory.

3. Sites, descriptions, and profiles

Logistics and accessibility resulted in slight limitation on the establishment of study sites, but not such that the results obtained here show major lacunae or bias. Observations have been derived from a wide variety of open shores and open or more exposed fjordic/sound situations on the islands of Borðoy, Eysturoy, Fugloy, Koltur, Kunoy, Mykines, Nólsoy, Sandoy, Streymoy, Suðuroy, Svínoy, Vágar, and Viðoy. The particular locations concerned are indicated on the island group map (Fig. 1). All visits were made during July and August, 1980.

In the following descriptive list, sites productive of supporting data only are in *italic*; more fully documented, especially profiled, locations are in **bold face**. Figure numbers in the lists refer to detailed profiles presented. The site order does not reflect sequence of working since, for clarity, sites have been re-ordered on a geographical basis.

Except in the case of the detailed Hoyvík transect area, intertidal profiles are not presented. As indicated above, we have accepted Børgesen's (1905) utilization of *Himanthalia* lower limits to mark the lower limit of his '*Littoral*' on open tidal coasts of adequate exposure to water movement. Elsewhere, the same limits can be represented by the upper limits of continuous dense laminarian growth (usually of *Alaria*), and these are mostly the highest level organisms of which the vertical limits appear on the profiles. Pools, creating upcarry of subtidal flora, are a separate matter in this context and we have adopted the same strategy as did Børgesen (1905), in dealing with that habitat in a different section where comments on additions or differences are required.


Fu
Vi
Ku
Bo
Sv
Ka
Ey
Str
Va
My
Ko
He
No
Sa
Sk
SD
LD
Su
1
2
3
4
5
6A
6B
7
8
9
10
11
12
13
14
15
16A
16B
17
18
19
20
21
22
23
24
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27
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31
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43
44

Fig. 1 Faroe Islands: open shore and comparative stations. Scale approx. 1 : 300 000.
For details of stations, see the numbered site list in the text. Numbers underlined represent profiled sites. Abbreviations of island names on the map represent the following:

Su = Suðuroy
LD = Lítla Dímun
SD = Stóra Dímun
Sk = Skúvoy
Sa = Sandoy
He = Hestur

Ko = Koltur
No = Nólsoy
Str = Streymoy
Va = Vágar
My = Mykines
Ey = Eysturoy

Ka = Kalsoy
Ku = Kunoy
Bo = Borðoy
Vi = Viðoy
Sv = Svínoy
Fu = Fugloy

Figs 2–10 General Notes.

Certain symbols and abbreviations are standard throughout the profiles covered by these figure numbers. All profiles carry bars representing the depth distributions for the site of all detected, or the most important, marine biota. Depths are always in metres, although the scales employed vary with quantity and style of data to be presented. Horizontal distances, where given, are also in metres. In some cases, standard symbols are augmented by pictorial symbols for further clarification; since the quantity and form of these vary between figures, they are detailed on the profile(s) concerned. For further development of these comments and the information background on which they depend, see the appropriate parts of the main text.

Standard symbols or abbreviations are as follows:

Taxa

Ad	*Antithamnion plumula* var. *demersum*
Ae	*Alaria esculenta*
An	*Ascophyllum nodosum*
Ap	*Ahnfeltia plicata*
Ba	Barnacles, in general
Bb	*Brongniartella byssoides*
Bc	*Balanus crenulatus*
Bp	*Bryopsis plumosa*
Bs	Brittle stars, in general
Ca	*Callophyllis cristata*
Cc	*Clathrina coriacea*
Cd	*Callithamnion decompositum*
Ce	*Ceramium shuttleworthianum*
Cl	*Callophyllis laciniata*
Cm	*Chaetomorpha melagonium*
Cn	*Callocolax neglectum*
Co	*Corallina officinalis*
Cr	*Ceramium rubrum*
Cs	*Callithamnion sepositum*
Da	*Desmarestia aculeata*
Dc	*Dilsea carnosa*
De	*Dermocarpa prasina* (= *Entophysalis conferta*)
Dl	*Desmarestia ligulata*
Dm	*Derbesia marina*
Ds	*Delesseria sanguinea*
Dv	*Desmarestia viridis*
Ec	Ectocarpoids, in general
Ee	*Echinus esculentus*
Ei	*Enteromorpha intestinalis*
Fd	*Fimbrifolium dichotomum*
Fl	*Furcellaria lumbricalis*
Gs	*Gigartina stellata*
Ha	*Halichondria*
He	*Himanthalia elongata*
Ho	*Halicystis ovalis*
Hr	*Hildenbrandia rubra*
Lc	*Lomentaria clavellosa*
Ld	*Laminaria digitata*
Lg	*Lithothamnion glaciale*
Lh	*Laminaria hyperborea*
Li	Lithothamnia, in general
Ll	*Leptophytum laeve*
Lo	*Lomentaria orcadensis*
Ls	*Laminaria saccharina*
Ma	*Membranoptera alata*
Mm	*Modiolus modiolus*
Od	*Odonthalia dentata*
Pa	*Palmaria palmata*
Pc	*Plocamium cartilagineum*
Pe	*Pseudolithoderma extensum*
Phc	*Phyllophora crispa*
Php	*Phymatolithon polymorphum*
Pht	*Phyllophora traillii*
Phtr	*Phyllophora truncata*
Pl	*Polysiphonia lanosa*
Pm	*Porphyra miniata*
Po	*Porphyra umbilicalis*
Pp	*Pterosiphonia parasitica*
Pr	*Phycodrys rubens*
Ps	*Ptilota serrata*
Pt	*Ptilota* spp.
Ptp	*Ptilota plumosa*
Pu	*Polysiphonia urceolata*
Pv	*Patella vulgata*
Sa	*Spongomorpha arcta*
Se	Serpulids, in general
Sp	Sponges, in general
Ul	*Ulva lactuca*
Ve	*Verrucaria* spp.

General symbols

l = epilithic
p = epiphytic } used in connection with taxa abbreviations or on distribution bars.
z = epizoic
in ( ), after l, p. or z (see above) = substrate types or 'host' organisms involved.
S = sand, in patches or stretches.
S G = blackish sandy gravel.

Symbols in distribution bar types

———————— = organism present in band-forming, 'forest', or otherwise dense growths (therefore common, abundant, or characterising).
– – – – – – – – = organism scattered, but consistent to occasional, over the depths concerned.
················· = organism present, but detected as very sparse to rare.

Site list

1. *Akraberg, south Suðuroy*. Subtidal. Dive off steep rocky head-and-cove type exposed shore beneath light-house. Clear water in 15 m depth. General algal collections on zoological dive.

2. *Beinisvort, south Suðuroy*. Intertidal. Gullies and faces of stacks just off-shore. Generally exposed positions.

3. *Trøllkonufingur, Skarvanes, Sandoy*. Intertidal. Åsen and Rueness. Tide-pools in rocky but not excessively steep shore. Pools showing strong upcarry of usually subtidal flora.

4. **Húsavík, Sandoy**. Intertidal and subtidal. Concrete-faced boulder harbour wall and steps. Broken boulders seaward of base of harbour wall (in 6 m) gave way to firm bedrock. At 10 m depth, gullies with sand and small stones penetrated the gently sloping bedrock. Latter completely covered by bare sand below 10 m.

5. **Sandur, Sandoy**. Subtidal and intertidal. Harbour wall of cemented vertical blocks faced with cement; base of wall at 7 m depth. Adjacent open sheltered rocks at and around low water level. Bouldered bottom below and to seaward of harbour wall in 7–12 m depths, with scattered and broken sandy patches. See Fig. 2. Also in Holt (1975).

6A. *Góðidrangur, Mykines*. Subtidal. Off rocky steep small islets west of Mykines, to 20 m depth.

6B. *Tindagjógv, Mykines*. Intertidal. Sloping rock with pools, north-west side of island.

7. *Borgagjógv, Mykines*. Subtidal. Vertical to slightly overhanging slab rock-face, with uneven large boulders on bottom below. All depths to 17 m.

8. *Skerhólmur, Sørvágsfjørður, Vágar*. Subtidal. Seaward face of exposed steep rocky islet. Collections from between 6/7 and 15 m depths.

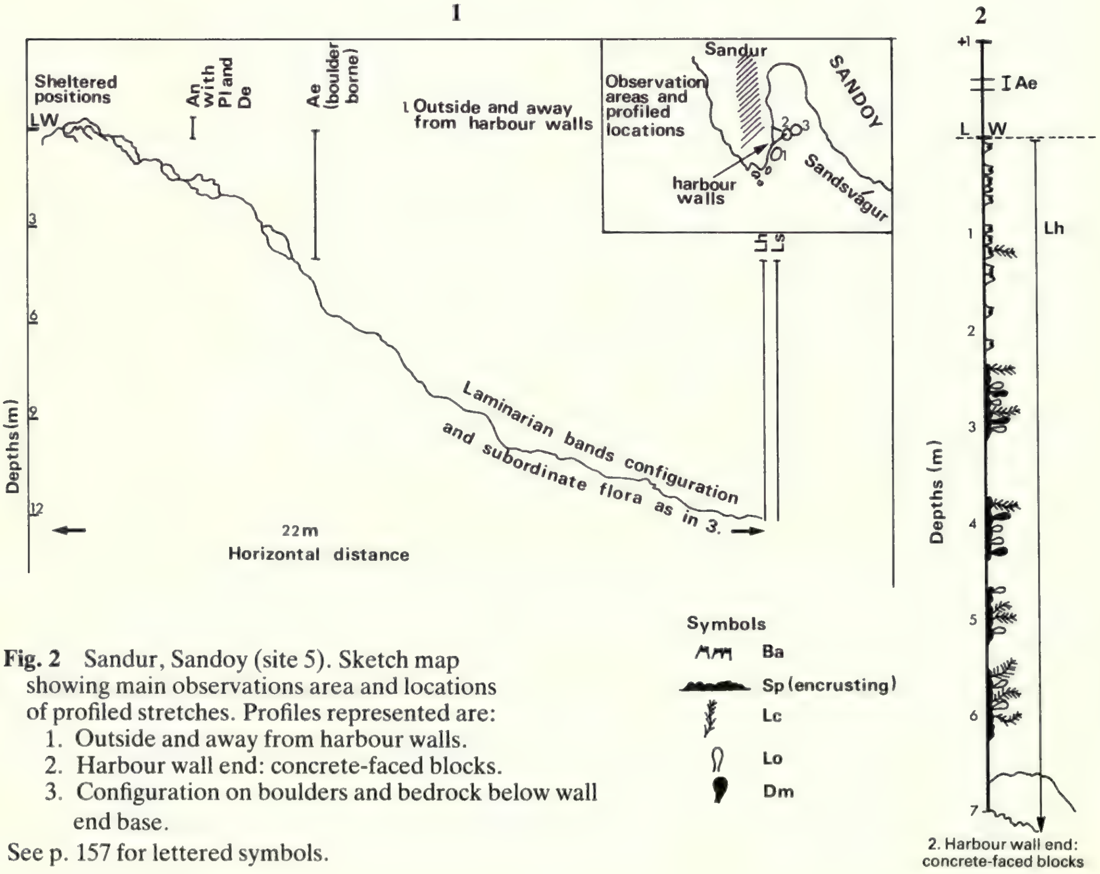
1
Sheltered positions
LW
An with Pl and De
Ae (boulder borne)
1 Outside and away from harbour walls
Observation areas and profiled locations
Sandur
SANDOY
Sandsvágur
harbour walls
2
3
1
Lh
Ls
3
6
9
12
Depths (m)
Laminarian bands configuration and subordinate flora as in 3.
22m
Horizontal distance
2
+1
Ae
L W
Lh
1
2
3
4
5
6
7
Depths (m)
2. Harbour wall end: concrete-faced blocks
Symbols
Ba
Sp (encrusting)
Lc
Lo
Dm

Fig. 2 Sandur, Sandoy (site 5). Sketch map showing main observations area and locations of profiled stretches. Profiles represented are:

1. Outside and away from harbour walls.
2. Harbour wall end: concrete-faced blocks.
3. Configuration on boulders and bedrock below wall end base.

See p. 157 for lettered symbols.

9. *Stack in Dragasund, opposite Tindhólmur.* Subtidal. Vertical face and easing slope/boulders below, in 5–9 m depths. South side exposed, north-west side less directly so.

10. *Oyrargjógv, Vestmannasund, Vágar.* Subtidal. Subtidal fringe and subtidal proper to 5 m depth. Strong water-flow, but less exposure than fully-open shores.

11. **Koltur, mid-north coast**. Subtidal. Barnacle-dominated exposed steep shore continuing subtidally initially as vertical cliff in shallower depths, with kelp forest to 12 m depth; easing slope and thinning kelp to 20 m depth. Bare rocks with a few crusts thence to 30 m depth. Details observations to 20 m, then general scan. See Fig. 3.

12. **Skriðutangi, north-east (seaward) shore of Nólsoy**. Subtidal. Detailed data to 32 m depth, more general below that to 40 m depth. Uneven but fairly steep exposed rock lacking laminarians other than fringing *Alaria* (1–2 m) and *Laminaria hyperborea.* Scattered plants of latter on easing slope between 10 and 20 m depths. True forest deeper than elsewhere, from 10 m to 20–22 m according to location. Firm rock and boulders to about 30 m, then scattered rocks amongst gravel substrata, with overlying or partly embedded small boulders down to and beyond 40 m; algae still then present. See Fig. 3.

13. **Kirkjubøur, point near Árnanes, Streymoy**. Intertidal, with observations on superficial subtidal. Exposed steep (but not high) cliffed headland of individually steep and fallen blocks, with gullies and upcarry niches at intervals. The steep cliffs generally continue descent as steeply to and into the subtidal; occasional very local areas form shallow intertidal shelves or shallowly but consistently subtidal shelves at fringe of cliffs. Downwash areas with easing slopes penetrate the boulders and narrow platforms. Headland grades to south into stones and boulders of the sheltered Kirkjubøur cove.

14. **Velbastaður, harbour wall and adjacent subtidal, Streymoy**. Subtidal. Detailed observations to 10 m depth, then more general scan beyond. Firm rock and boulders, penetrated throughout (in 2 m and below) by gullies where slope eases.

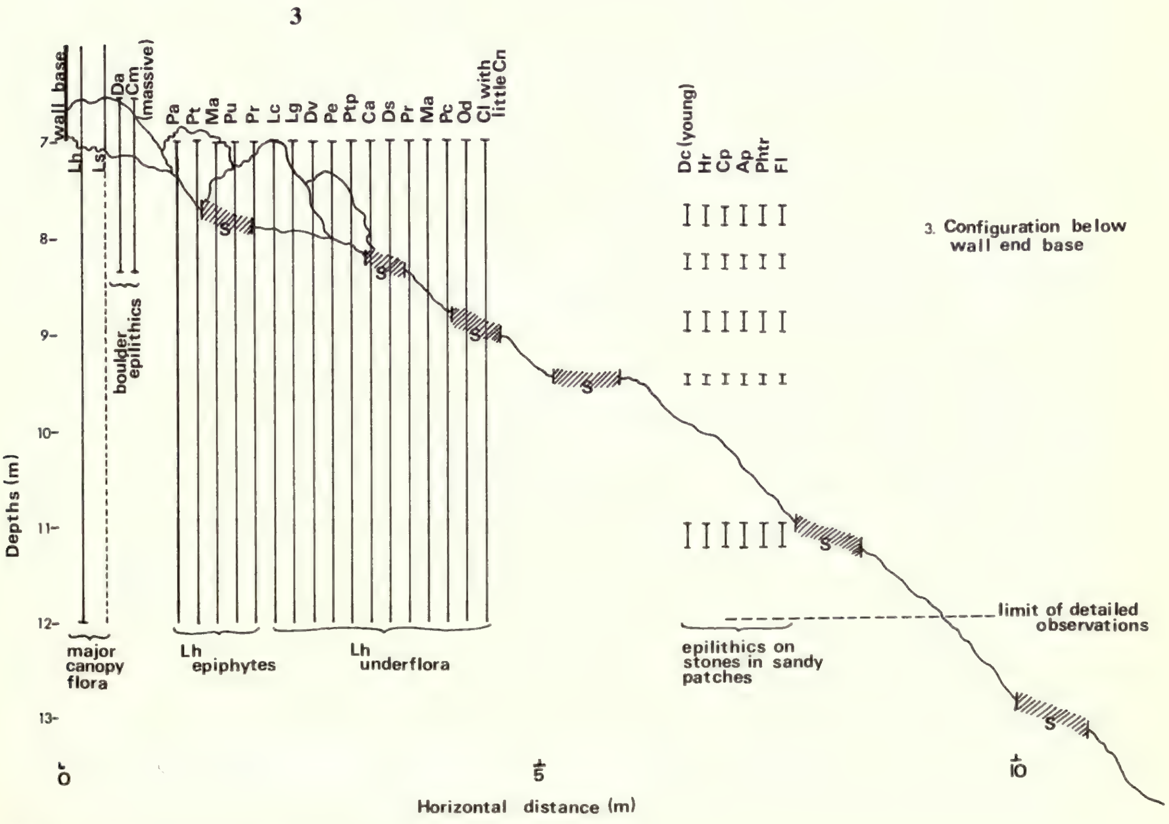
3
wall base
Lh
Ls
Da
Cm
(massive)
Pa
Pt
Ma
Pu
Pr
Lc
Lg
Dv
Pe
Ptp
Ca
Ds
Pr
Ma
Pc
Od
Cl with little Cn
Dc (young)
Hr
Cp
Ap
Phtr
Fl
boulder epilithics
S
S
S
S
S
S
3. Configuration below wall end base
limit of detailed observations
major canopy flora
Lh epiphytes
Lh underflora
epilithics on stones in sandy patches
Depths (m)
7
8
9
10
11
12
13
0
5
10
Horizontal distance (m)

Fig. 2 (cont.) Caption, see p. 158.

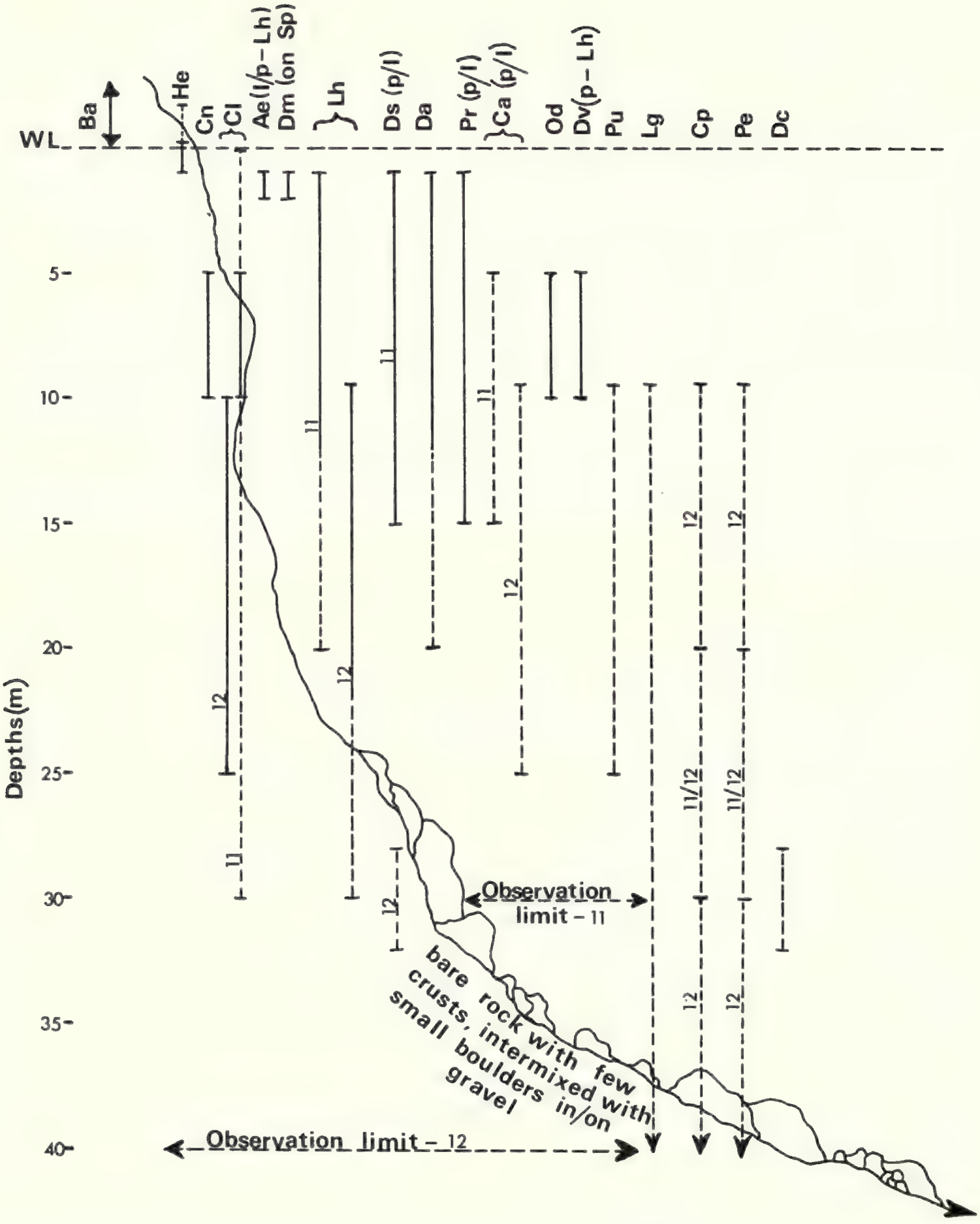

Fig. 3 Semi-diagrammatic composite showing structure of steep exposed subtidals and distribution of biota present. Based on data from sites 11 (Koltur) and 12 (Nólsoy). No distinctions between sites, or absence of the organism from one site—bars plain; critical differences between site patterns—bars appropriately numbered. See p. 157 for symbols.

15. **Argir, south of Tórshavn, Streymoy**. Intertidal. Semi-exposed moderately-sloping firm rock slab and bedrock shore, with occasional small boulder overlay. Penetrated by runnels and upcarry/downwash areas. Dense *Alaria* fringe; locally sheltered niches with good *Fucus spiralis*. Laminarians in adjacent small harbour.

16A. *Hospital Rocks, Tórshavn, Streymoy*. Intertidal. Minor low headland of smooth rock slabbing with downwash channels, swell channels, pools, and a flat inwash area on north side of outer point. Occupies north side of the inner depths of the haven, just south of the sewage pipe and mole below hospital.

16B. *Tinganes, Tórshavn, Streymoy*. Intertidal, with shallow subtidal observations. Gently sloping firm rock and artificial facings (at intervals), on central headland in Tórshavn harbour; usually pollution pattern associated with functional port. Presumably the same as the station in Rex (1970) and close in position to Holt's (1975) station Tinganeset.

17. *Shore below Old Fort, north Tórshavn, Streymoy*. Intertidal. Rocky shore with sheltered to semi-exposed rock tongues, contained coves, and pools, just north of mole enclosing ferry and unloading harbour areas. Shore slopes rather gentle. Approximately the position of Holt's (1975) station Skansen.

18. **Tórshavn, heads and coves to north, between Old Fort Head (station 17) and coves/heads transect area, Hoyvík (station 19), all Streymoy**. Intertidal, with shallow subtidal observations. Semi-exposed, mainly gently-sloping, bedrock headlands, with contained gullies, pools, lagoons and channels. Only local detrital and broken loose rock areas. Flora a mosaic, but some accepted major exposure indicators locally present. Coves and inlets between heads rather more sheltered, but carrying exposure indicators (e.g. *Himanthalia*) alongside shelter indicators (e.g. *Ascophyllum,* massive *Laminaria saccharina*).

19. **Hoyvík, coves and headlands, Streymoy**. Subtidal and intertidal. Detailed transects on and seaward from semi-exposed firm rock minor headland. Comparative observations intertidally and subtidally in adjacent more sheltered coves to north and south. See Fig. 4. Close to one of the stations in Rex (1970).

20. **Hoyvík, opposite Byrgistangi islet, Streymoy**. Intertidal, with shallow subtidal observations. Pools and shallow subtidal along south side of firm rocky headland, semi-sheltered, north of station 19. Flora an equivocal mosaic of exposure and shelter characteristics. Pools and shaded undercut verticals showing considerable subtidal upcarry.

21. *Eystnes, Eysturoy*. Subtidal. Dive off steep firm rocky shore at the mouth of the Tangafjørður, east of and opposite Hvitanes. Firm rock substrate slope eases as depth increases. Strong *Laminaria hyperborea* forest in first 10 m, opening out to smaller and sparser plants below. Algal growth continuing on rock below dive limit (24 m) at which depth red underflora was not well-developed.

22. *Stórafles*. Subtidal. Isolated rock in the middle of Tangafjørður mouth. Dive to 20 m over steep but shallowing rock slope bearing *Laminaria hyperborea* forest in upper half of penetrated depths.

23. **Raktangi and Abbin, Eysturoy**. Intertidal with shallow subtidal observations. Peninsula tip and rocks lateral on east (Skálafjørður) side of headland. Largely exposed or semi-exposed flora in wash channels, on rock slabbing, on undercut sheer rock, on fallen boulders and in retained pools. Considerable subtidal upcarry in shaded standing water. Shallow subtidal wave-washed edges with mosaic exposed flora. Sheltered-water flora on some locally protected mobile substrata. *Alaria* and *Ascophyllum* noted growing side-by-side. *Modiolus* near peninsula tip.

24. **Kvívík, Streymoy**. Subtidal. Sloping rock surface penetrated by shallow subtidal channels in bedrock, leading to upcarry of the dominant *Laminaria hyperborea* forest; latter continuing down to 8/9 m depth, where slope levelled off. Quite extensive sand-covered intrusive gullies in depths of 4 to 8 m; deeper gullies tended to be bare of algae. Bedrock scored by niches and locally with boulders in declivities and gullies. *Modiolus* clumps at bedrock/boulder/gully boundaries and in the bedrock niches. Dive terminated at 9 m.

25. **Sundini, under middle span of bridge, near Norðskali, Eysturoy-Streymoy**. Subtidal. Comparative station deep into sound between the two islands. Included because of characteristics—sheltered as to wave-action but aping exposure through very fast tidal current effects. Total available depths 5 to 7 m, according to location. Solid bedrock, with small overlying boulders. Luxuriant *Alaria* mixed patchily with *Laminaria hyperborea*. Locally equal admixture of *Laminaria faeroensis*, with thick stipes and long blades. Generally impoverished underflora and epiphytes. *Echinus* and asteroids in fair abundance.

26. *Sakshøvn, south side, 200 m seaward of Grótdalsgjógv, Streymoy*. Intertidal and shallow subtidal. Narrow and smoothly steep shaded intertidal descending in about 2 m or locally less beneath the sand/silt substrate forming the lateral base of the haven. Deep cut and high overhangs from above, with continuous off-fall of strong freshwater flow. Restricted and specialized sheltered-water flora. See also Holt (1975) and Rex (1970), both of whom examined parts of the same haven.

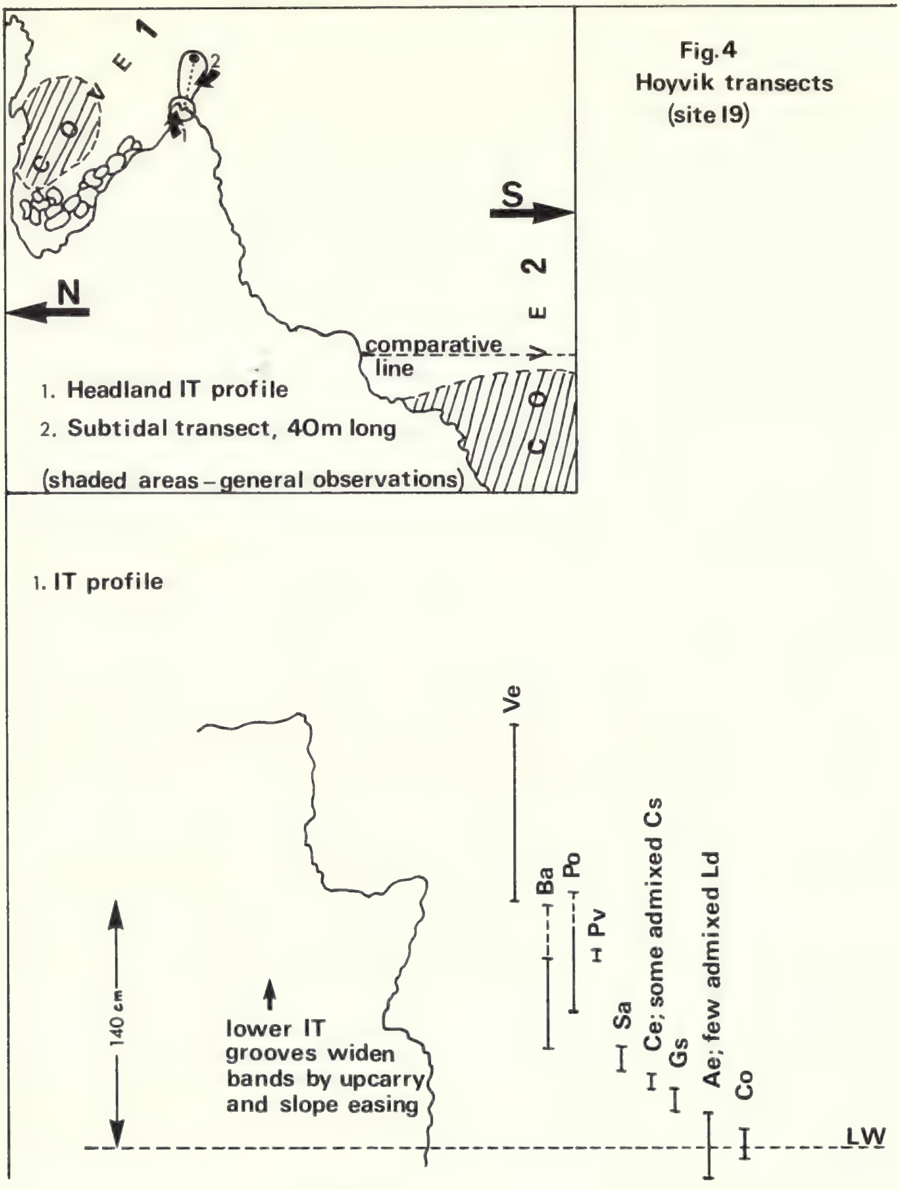
Fig. 4
Hoyvik transects
(site 19)
COVE 1
2
1
S
N
COVE 2
comparative line
1. Headland IT profile
2. Subtidal transect, 40m long
(shaded areas – general observations)
1. IT profile
Ve
Ba
Po
Pv
Sa
Ce; some admixed Cs
Gs
Ae; few admixed Ld
Co
140 cm
lower IT grooves widen bands by upcarry and slope easing
LW

Fig. 4 Caption, see p. 163.

27. *Eiði, harbour wall (south) side, within the artificial mole, Eysturoy*. Subtidal. Mole wall of large broken boulders, grading out in 9–10 m depths to blackish shell-sand having only diatom cover. Sheltered-water flora.

28. *Eiði, open (north) side, beyond the inland lake; strong wave-action; Eysturoy*. Subtidal. *Laminaria hyperborea* forest in 5 to 7 m; oldish plants on bedrock, with density varying mosaically. Sandy patches overlying bedrock in places; large boulders overlying bedrock elsewhere in places. Water movement above 5–7 m too strong for significant observations.

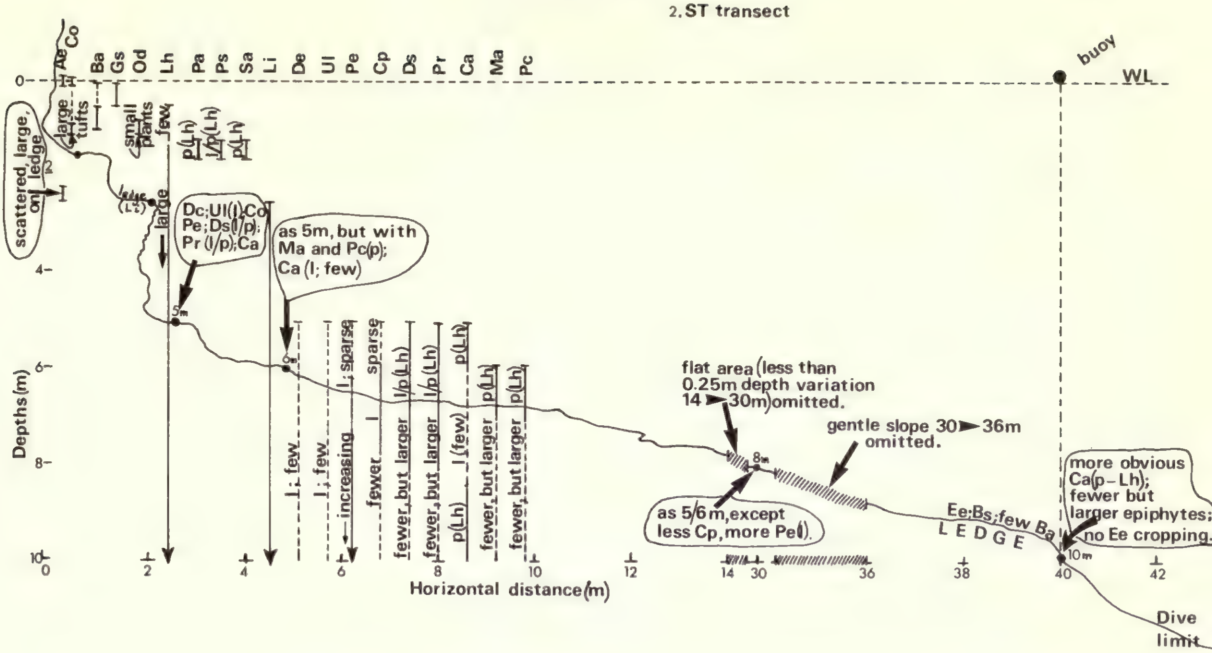
2. ST transect
Ae Co Ba Gs Od Lh Pa Ps Sa Li De Ul Pe Cp Ds Pr Ca Ma Pc
buoy
WL
0
4
6
8
10
Depths (m)
scattered, large, on ledge
large tufts
small plants
few
large
ledge
p(Lh)
l/p(Lh)
p(Lh)
Dc;Ul(l);Co Pe;Ds(l/p); Pr (l/p);Ca
as 5m, but with Ma and Pc(p); Ca (l; few)
5m
6m
l ; few
l ; few
increasing
l ; sparse
fewer
sparse
fewer, but larger
l/p(Lh)
fewer, but larger
l/p(Lh)
p(Lh)
l (few)
p(Lh)
fewer, but larger
p(Lh)
fewer, but larger
p(Lh)
flat area (less than 0.25m depth variation 14 ► 30m) omitted.
gentle slope 30 ► 36m omitted.
8m
as 5/6 m, except less Cp, more Pe(l).
Ee;Bs;few Ba
LEDGE
more obvious Ca(p–Lh); fewer but larger epiphytes; no Ee cropping.
10m
Dive limit
0
2
4
6
8
10
12
14
30
36
38
40
42
Horizontal distance (m)

Fig. 4 Hoyvík (site 19). Transect and observational area sketch map showing positions of profiles and limits of Cove 1 and Cove 2 general observational and comparative areas. Profiles cover (1) intertidal patterns, and (2) subtidal patterns. See p. 157 for symbols.

29. **Near Stakkur, north-west coast of Streymoy**. Subtidal and intertidal. Very steep to vertical cliff descending to 23 m depth and then levelling off to rough boulder-strewn bottom, latter with no evidence of even crustose algae. No true 'forest', but *Laminaria hyperborea* plants present from 8 to 15 m depths. Very strong west-to-east running tidal stream during dive; if consistent, may have influence on state and distribution of flora. See Fig. 5.

30. **Below and west of Kollur peak, north-west Eysturoy**. Subtidal. Similar steeply-sloping rocks to those of station 29, but showing more irregularity than there and the overlying boulders larger and more irregular. *Laminaria hyperborea* forest over depth range 10–16 m, with plants still present at depths well beyond that. See Fig. 6.

31. **Gjógv, north-east Eysturoy**. Subtidal and intertidal. Deep (175 m long) cleft into the solid bedrock of the exposed northern shore; shows gradation of effects of configuration, depth, substrate type and water-movement as inter-relatedly determinating species presence, density and distribution along and throughout the cleft. Comparative transect also examined in the subtidal of the vertical to steep rock face outside the cleft to the north. South side with similar but lesser steep face and with additional off-cliff shallowly-sloping seaward slabbing and retained pools, all fairly well exposed to strong wave-wash and intertidally largely animal-dominated. Grades into bouldered cove on south. See Fig. 7.

32. **Elduvík, Funningsfjørður, Eysturoy**. Intertidal with some subtidal observations. Subsidiary small cove on open south coast of the wide mouth area of this fjord; studies on bedrock and large boulder strewn, fairly steep, shores of both east and west sides. Pools on both sides of cove, the west (Litlanes) showing larger and richer low water level pools and channels, protected by the immediate off-lying large rocks taking main wave impact. Subtidal of east side examined to 4 m depth within the cove; substrate a continuation of the large boulder strewn aspect of the intertidal.

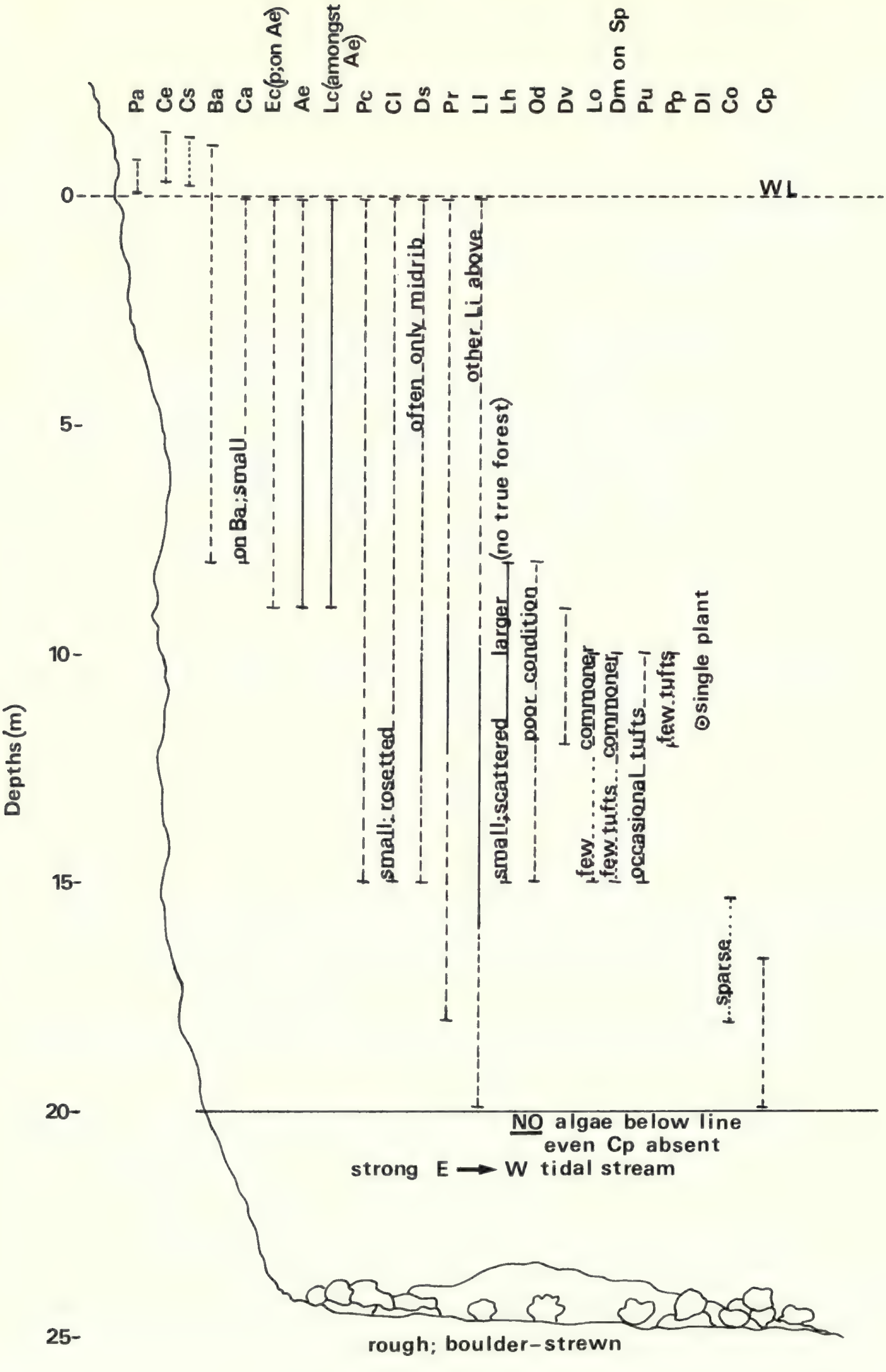

Fig. 5 Near Stakkur, Streymoy (site 29). Very steep subtidal cliff-face showing certain unusual characteristics of distribution. Detailed comments in appropriate parts of main text. See p. 157 for symbols.

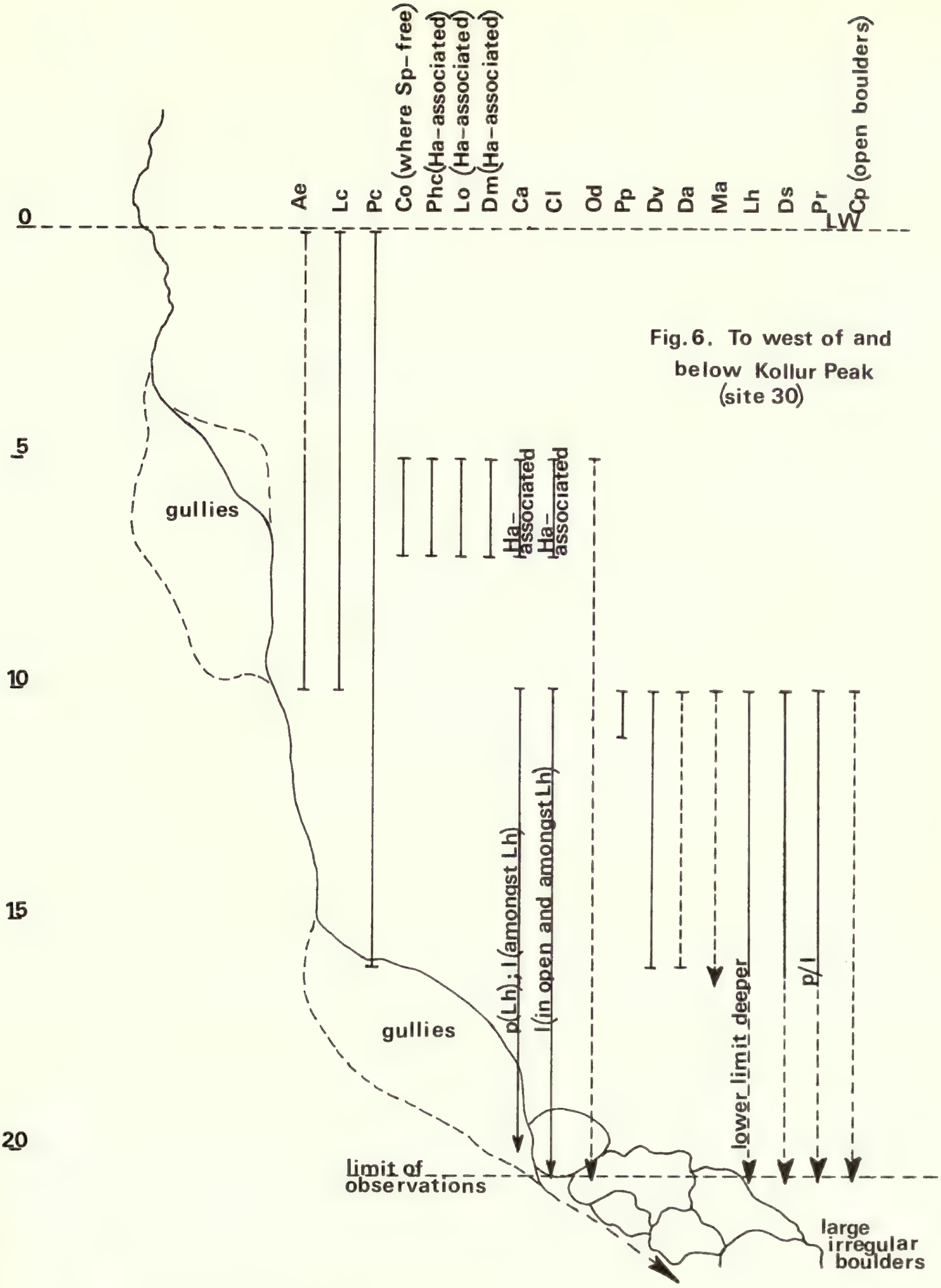
Fig. 6. To west of and below Kollur Peak (site 30)
0
5
10
15
20
Ae
Lc
Pc
Co (where Sp–free)
Phc(Ha–associated)
Lo (Ha–associated)
Dm(Ha–associated)
Ca
Cl
Od
Pp
Dv
Da
Ma
Lh
Ds
Pr
Cp (open boulders)
LW
gullies
Ha–associated
Ha–associated
p(Lh); l (amongst Lh)
l (in open and amongst Lh)
lower limit deeper
p/l
gullies
limit of observations
large irregular boulders

Fig. 6 Below and west of Kollur Peak, north-west Eysturoy (site 30). For physical distinctions from site 29 (see Fig. 5), see comments in the site list descriptions. Sponge-associations, a facet of the biota here and elsewhere, are discussed in a special section of the text. See p. 157 for symbols.

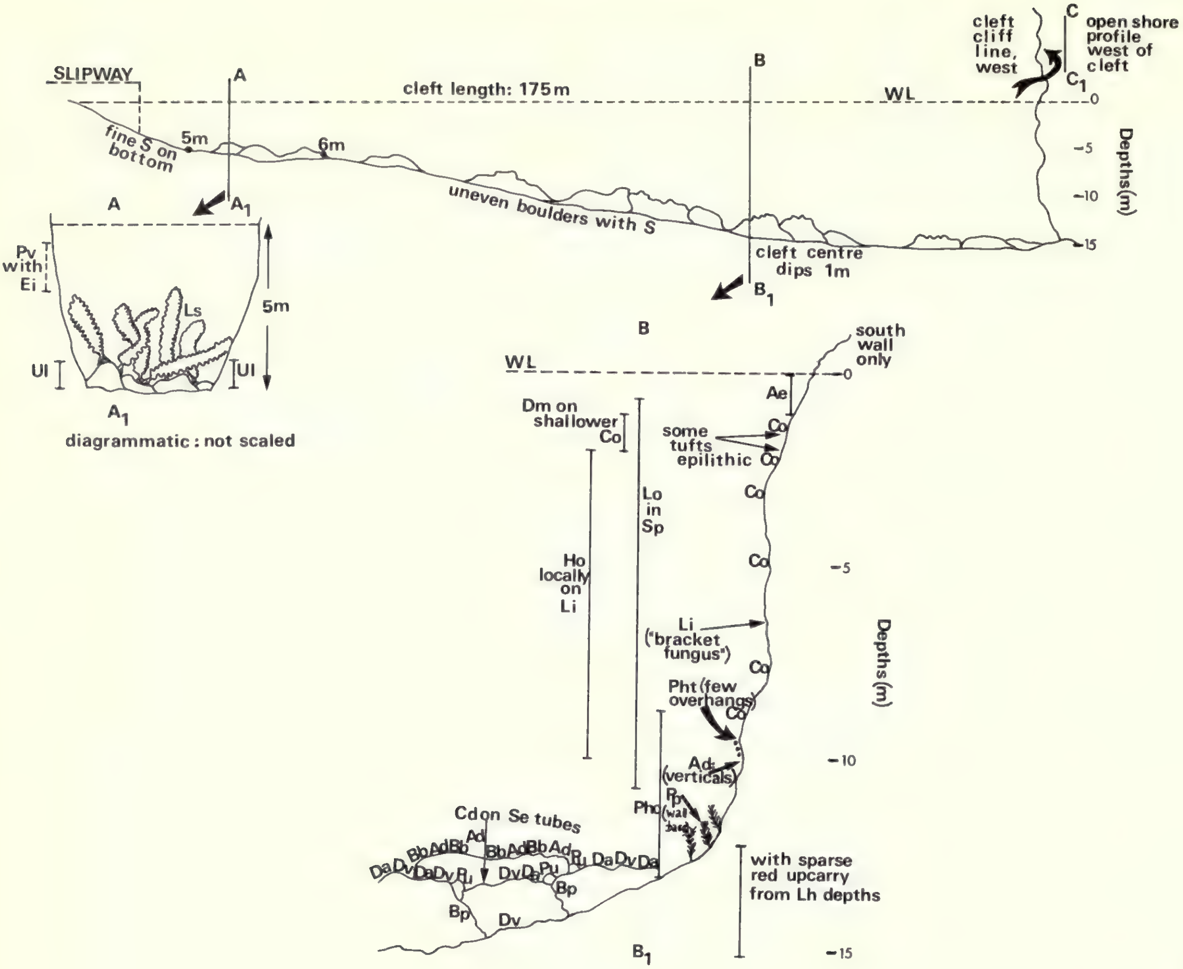
SLIPWAY
A
cleft length: 175m
B
WL
cleft
cliff
line,
west
C
C1
open shore
profile
west of
cleft
0
-5
-10
-15
Depths (m)
fine S on bottom
5m
6m
uneven boulders with S
A1
cleft centre
dips 1m
B1
A
Pv
with
Ei
Ls
Ul
Ul
5m
A1
diagrammatic : not scaled
B
south
wall
only
WL
0
Ae
Dm on
shallower
Co
some
tufts
epilithic
Co
Co
Co
Co
Lo
in
Sp
Ho
locally
on
Li
-5
Li
("bracket
fungus")
Co
Depths (m)
Pht (few
overhangs)
Co
-10
Ad
(verticals)
Rp
(wall
base)
Pho
Cd on Se tubes
Ad
Bb Ad Bb
Bb Ad Bb Ad
Pu
Da Dv Da
Da Dv Da Dv Pu
Dv Da Pu
Bp
Bp
Dv
with sparse
red upcarry
from Lh depths
B1
-15

Fig. 7 Gjógv (site 31). Plan of the Cleft, indicating the positions of the profiled sections A—A$_1$; B—B$_1$; C—C$_1$ (the latter outside the Cleft, to the west). Special characteristics of biota distribution are discussed throughout appropriate sections of the main text. See p. 157 for symbols.

33. **Oyndarfjørður, Eysturoy**. Intertidal and subtidal. North side of this short open fjord; intertidal of the two minor flat headlands and broken/bouldered flats at south end of the village. Rich intertidal flora, showing principally only moderately sheltered aspect with local mosaics of rather greater exposure, especially in damp shaded continuous wash areas. Shallow subtidal between the two minor heads showed standard *Laminaria hyperborea* 'forest', with penetrating sandy gullies in 2–3 m depths. Some sand-buried species, but the majority on bedrock under the forest, as epiphytes, or on sand-embedded boulders/stones.

34. **Off Kúvingafjall, west coast of Kunoy, Kalsoyarfjørður**. Subtidal. Very steep to vertical, ledged, rock face down to about 8–10 m; penetrated at lower depths by gullies with boulders in the bases, and by clefts with sandy bottoms. Slope eases markedly at about 8–10 m, where substrate changes to bedrock with many sandy channels and gullies, all overlain by boulders. Dive limit 16 m. *Laminaria hyperborea* forest present over 3–16 m depths and beyond. See Fig. 8.

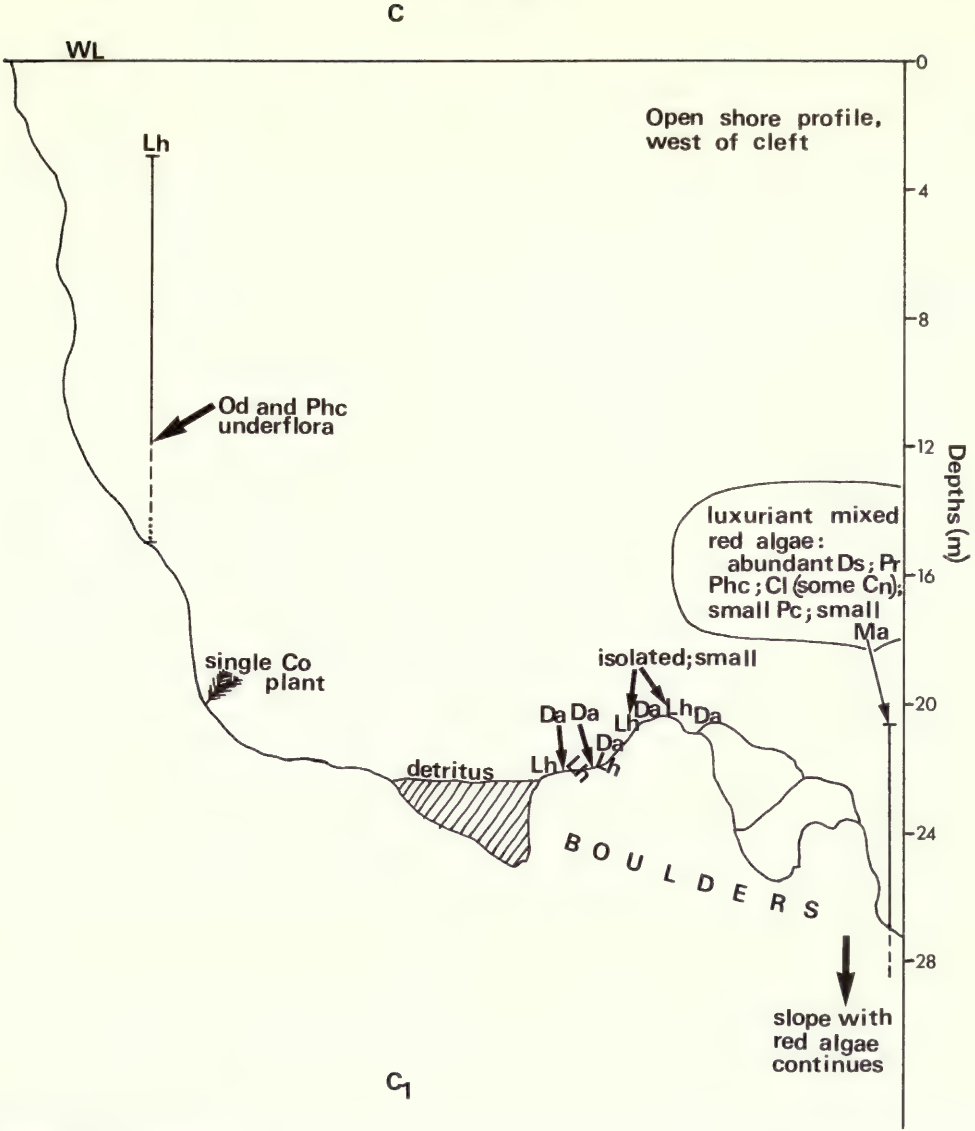
C
WL
0
4
8
12
16
20
24
28
Depths (m)
Open shore profile, west of cleft
Lh
Od and Phc underflora
luxuriant mixed red algae: abundant Ds; Pr Phc; Cl (some Cn); small Pc; small Ma
single Co plant
isolated; small
Da Da
Lh
Da
Lh
Da
Lh
Da
Lh
Da
Lh
detritus
BOULDERS
slope with red algae continues
C1

Fig. 7 (cont.) Caption see p. 166.

35. **Ánir and adjacent narrows, Haraldssund, Borðoy-Kunoy**. Intertidal and subtidal (shallow only). Front of boathouses, north of Klaksvík. Concrete and old metal intertidal and subtidal surfaces, with small boulders buried in dark sand. Downflow of freshwater across a few intertidal strips. Potentially strong throughflow of tidal water in the sound, but shore appears largely to be a sheltered one; *Alaria, Laminaria hyperborea* and *Ascophyllum nodosum* locally juxtaposed.

Deeper subtidal at point in centre of narrows just north of Strond (Borðoy) and Haraldssund (Kunoy). No real forest of *Laminaria hyperborea*; only scattered small plants at 10–20 m depths. Substrate largely small rocks, boulders, and stones embedded in dirty loose layer of sand and gravel; occasional bedrock outcrops. *Modiolus* throughout. Observations between 10 and 30 m depths.

36. *Hvannasund (Leiti), Viðoy*. Intertidal and subtidal. Narrow intertidal rocky fringe of irregularly-surfaced slabbing, varying from smooth domes to much-dissected and stream-incised stretches carrying pools and wash-channels. Shallow subtidal with similar configuration, grading into gravel with embedded shells and stones; *Modiolus* abundant throughout. *Laminaria hyperborea* present over range (3–)5–15 m; epiphytes and red underflora dense on stipes and stones.

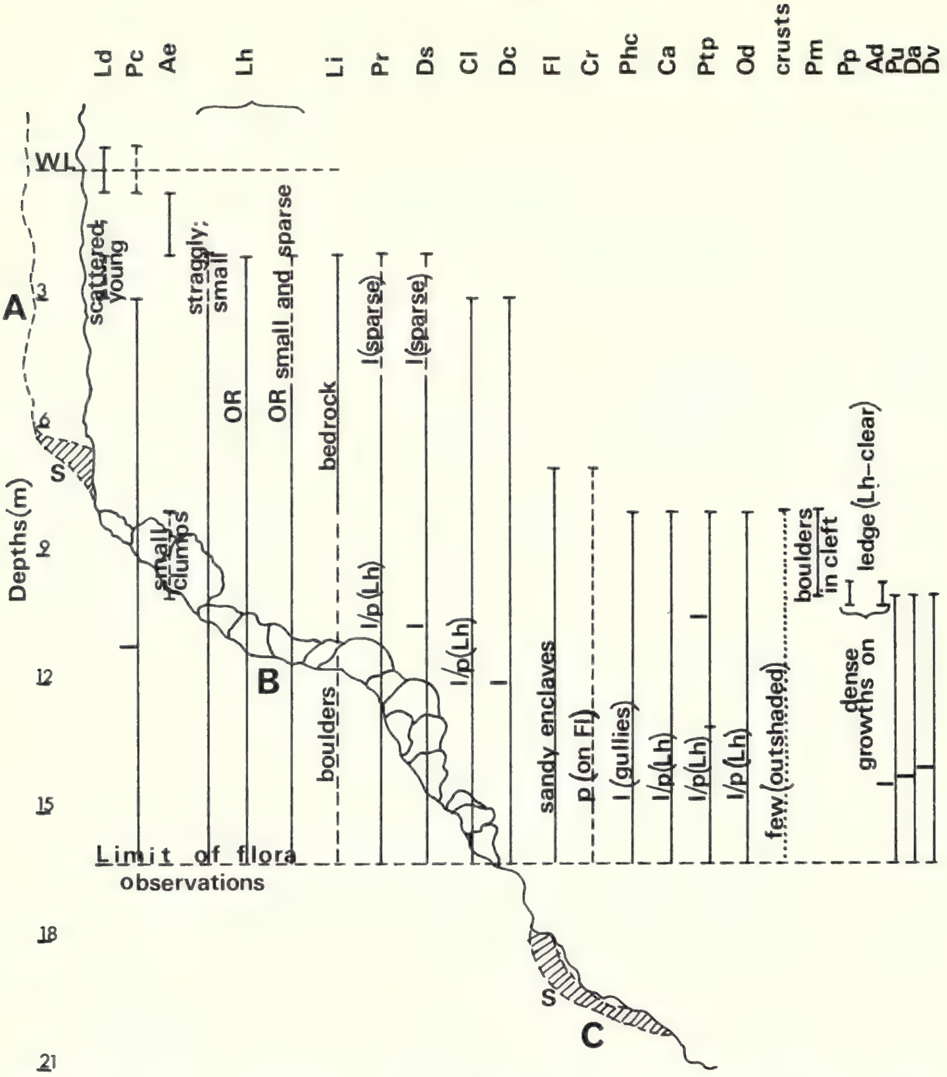
Ld
Pc
Ae
Lh
Li
Pr
Ds
Cl
Dc
Fl
Cr
Phc
Ca
Ptp
Od
crusts
Pm
Pp
Ad
Pu
Da
Dv
WL
A
S
B
S
C
Depths (m)
3
6
9
12
15
18
21
scattered; young
straggly; small
OR
OR small and sparse
bedrock
l (sparse)
l (sparse)
small clumps
l/p (Lh)
l/p (Lh)
boulders
sandy enclaves
p (on Fl)
l (gullies)
l/p (Lh)
l/p (Lh)
l/p (Lh)
few (outshaded)
boulders in cleft
ledge (Lh–clear)
dense growths on
Limit of flora observations

Fig. 8 Off Kúvingafjall, Kalsoyarfjørður, west Kunoy (site 34). Subtidal profile of the ledged and varyingly sloped rock face and overlying substrates, described in the site list. Substrate symbols represent as follows:

A = Li-covered, almost vertical, rock penetrated by vertical clefts with sandy bottoms and inner erosion caves.

B = Boulders on detritus, with sand channels between, to 16m depth.

C = Bedrock with sand channels.

See p. 157 for other symbols.

37. **Viðareiði, Viðoy**. Intertidal and shallow subtidal. Firm rocky promontories of moderate slope, west side of island, near church. Draining surfaces, strong upcarry channels, and pools present. Occasional deep clefts in shallow subtidal (see station 38) and upstanding protective off-shore or bottom shore rocky knolls at lower shore levels. Freshwater downflow over some parts of intertidal. Usual major brown subtidal flora (see station 38).

38. **Viðareiði, Viðoy; central cleft, west side**. Subtidal and intertidal. Deep incut cleft in firm bedrock of centre of the promontory area (see station 37). Strong swell and wave-run creating greater scour on north side than on south. Firm steep rocky sides terminating in 7 m depth in a gravel and silt base bearing

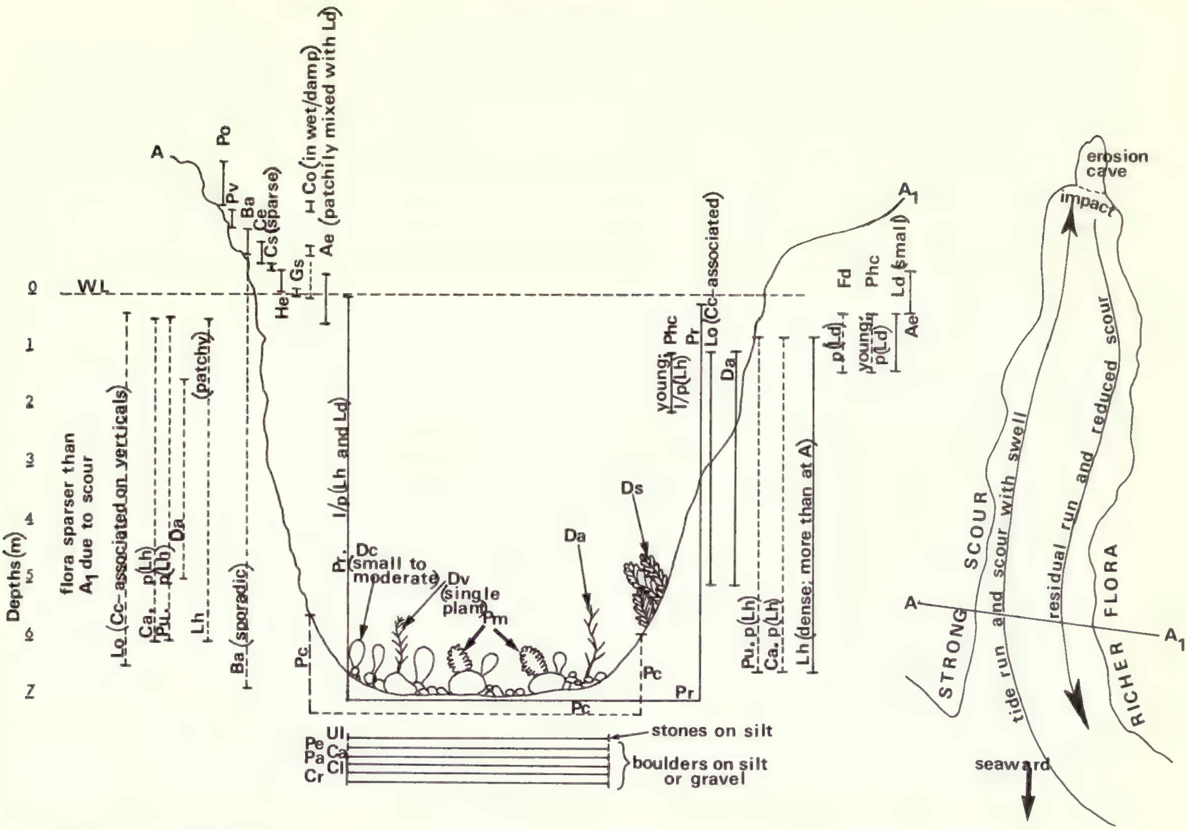
A
A₁
WL
Depths (m)
0
1
2
3
4
5
6
7
flora sparser than A₁ due to scour
Lo (Cc–associated on verticals)
Ca. p(Lh)
Pu. p(Lh)
Da
Lh
(patchy)
Ba (sporadic)
Pc
Po
Pv
Ba
Ce
Cs (sparse)
He
Gs
H
H Co (in wet/damp)
Ae (patchily mixed with Ld)
I/p(Lh and Ld)
Pr
Dc (small to moderate)
Dv (single plant)
Pm
Da
Ds
young; I/p(Lh)
Phc
Pr
Lo (Cc–associated)
Da
Pu. p(Lh)
Ca. p(Lh)
Lh (dense; more than at A)
p(Ld)
Fd
young; p(Ld)
Phc
Ld (small)
Ae
Pc
Pr
Pc
Ul
Pe
Ca
Pa
Cl
Cr
stones on silt
boulders on silt or gravel
erosion cave
impact
STRONG SCOUR
tide run and scour with swell
residual run and reduced scour
RICHER FLORA
seaward

Fig. 9 Central Cleft, Viðareiði (site 38). Comparative distribution around base and both sides of the differentially scoured and wave-run affected cleft. Position of the detailed transection indicated on the semi-diagrammatic sketch plan of the whole cleft. See p. 157 for other symbols.

boulders and stones. *Laminaria hyperborea* forest on south side; richer in cover, species and individual luxuriance than north. Narrow intertidal with patchy coverage on steep areas. Overall slightly calmer than surrounding wave-beaten coast, despite the swell and wave-run. See Fig. 9.

39. *Hamarsgjógv, north of Eiðsvík, Viðoy (= Viðareiði, east side)*. Intertidal and subtidal. Intertidal chiefly of concrete steps of Eiðsvík slipway, bearing rich flora; subtidal on steep rock in 5 to 7 m depth, bearing *Laminaria hyperborea* forest. Configuration uneven. Collections from rock and of epiphytes.

40. *Marknagjógv cave, east Viðoy*. Intertidal and shallow subtidal. Boat collection from walls and accessible parts of roof of large, deep, shaded cave (to 4 m above waterline); strongly swell-affected, causing continual wetting to high level and roof spray. Animal-dominated lower bands, due to light reduction and strong wave-run.

41. *Havnartangi, Svínoy*. Subtidal. Substrate of large boulders, rocks, and very steep to vertical surfaces of bedrock. Large boulders in 5 to 9 m depths bearing *Laminaria hyperborea* forest. Flora showing little variation over 1 to 9 m depths, with very sparse red flora on verticals.

42. **Svínoyareiði, Svínoy.** Intertidal and shallow subtidal. Flat rock-slabbing shores, stepping and shelving to low water level and beyond, north and south of landing stage, west coast to north side of Svínoyareiði. Many dissected and draining surfaces; deep to shallow and wide pools, some in shade between upstanding knolls of protective rock at lower levels of the shore. Few deep incut caves with dripping freshwater, behind main shore line. Overall a semi-exposed shore, but with wavewash or swell most of the time. Subtidal shows usual shallow-water dominance by large forms on the mainly firm substrata. Upcarry of subtidal flora into large, deep and shaded, pools. A shore stretch close to this site was examined by Holt (1975).

43. *Promontory in Scarðsvik, Fugloy*. Intertidal only. Collection by boat from steep rock surface; animal-dominated exposed rocky shore throughout.

44. **Svøðutangi, north Fugloy**. Subtidal. Exposed rock standing offshore. Initially steep, fairly soon (in 12 to 15 m) shelving and easing, firm bedrock surface overlain in 15 to 29 m by large boulders of house-size. Latter lie on other large embedded boulders in blackish sandy gravel where that intrudes as patches and tongues over bedrock. Extensive barnacle (*B. crenulatus*) cover, reaching 100% of surface on horizontals of boulders. *Laminaria hyperborea* forest shows reduction in density, plant size, and epiphyte numbers with depths between 15 and 29 m. See Fig. 10. Note that the south-eastern bay (Hattarvík) on Fugloy was examined by Holt (1975).

The inclusion of certain other sites examined at Nes (Tangafjørður) and Hvitanes (Kaldbaksfjørður entrance, described by Børgesen, 1905: 694, as carrying a '. . . perfect "open sea" algal vegetation . . .') would have been appropriate for comparative purposes but for two reasons: (i) both are situated in areas close to open-shore sites and with existing, more appropriate, comparative sites of similar characteristics; (ii) both are described in some detail by Tittley *et al.* (1982).

4. Results: comparative species distributions

The visually more impactful (level-, band-, or zone-characterizing) organisms in shore and subtidal populations are so because of unusual size, morphology, density of growth, or consistent association with certain recognizable combinations of environmental conditions. Consistency of association with environmental conditions is always comparative, not absolute: epiphytic species generally, if less abundantly, also occur epilithically; underflora species beneath the canopy are rarely consistently so, usually also appearing away from the canopy dominants, or epiphytically on the canopy, or both; species characteristically associated with particular subtidal or intertidal levels below and above Chart Datum commonly, if variably densely, occur also elsewhere. Thus, very few species are entirely intertidal, very few entirely

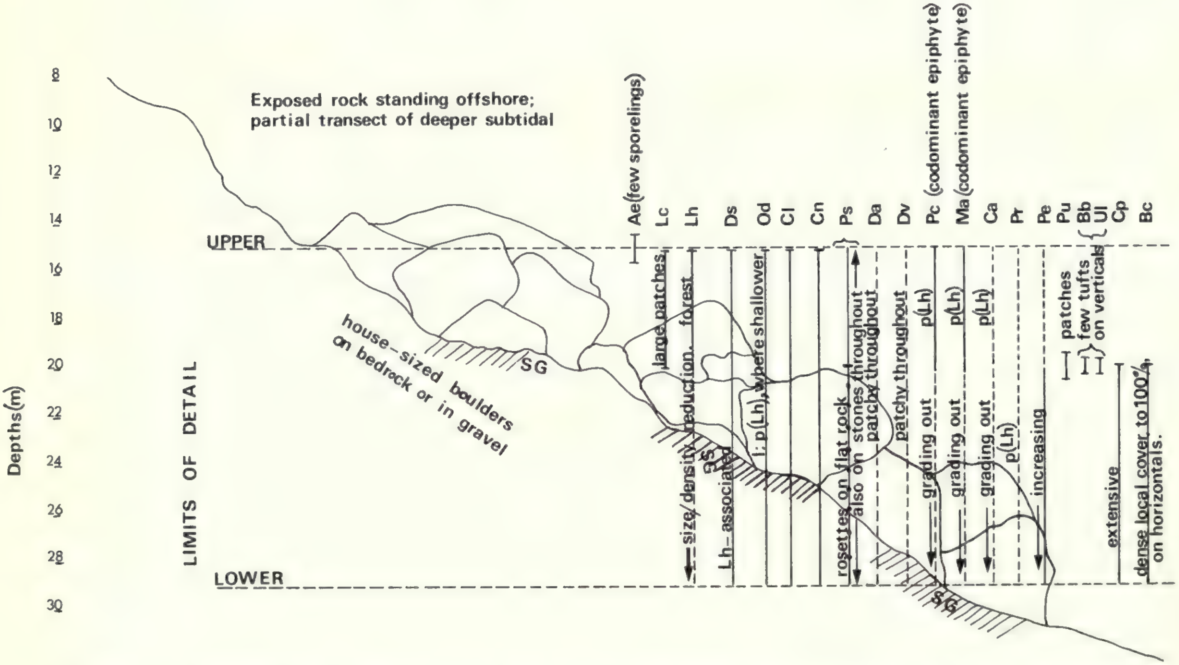
Depths(m)
8
10
12
14
16
18
20
22
24
26
28
30
Exposed rock standing offshore; partial transect of deeper subtidal
UPPER
LOWER
LIMITS OF DETAIL
house-sized boulders on bedrock or in gravel
SG
SG
SG
Ae(few sporelings)
Lc
Lh
Ds
Od
Cl
Cn
Ps
Da
Dv
Pc (codominant epiphyte)
Ma (codominant epiphyte)
Ca
Pr
Pe
Pu
Bb
Ul
Cp
Bc
large patches
forest
size/density reduction
Lh-associated
l: p(Lh), where shallower
rosettes on flat rock
also on stones throughout
patchy throughout
patchy throughout
p(Lh)
p(Lh)
p(Lh)
p(Lh)
grading out
grading out
grading out
increasing
patches
few tufts
on verticals
extensive
dense local cover to 100%, on horizontals.

Fig. 10 Svøðutangi, north Fugloy (site 44). Detailed profile and distributions of subtidal deeper levels only, with unusual characteristics indicated on profile and/or in site description. See p. 157 for symbols.

subtidal, although the extent and frequency of occurrence may be much greater in the one milieu than the other. Species that *are* comparatively consistent tend to be utilized as the indicators of their preferred situations and it is primarily such species, rather than interesting rarities, that receive comment here. The interesting rarities and their distributions are summarized alongside more frequent species in Table 4, and comments appear as appropriate throughout later parts of this text.

i. Subtidal: major organisms

Alaria

This, generally the uppermost major organism specific to the subtidal, shows considerable consistency in appearance, depths colonized, and conditions tolerated, in the Faroes. It is generally less confined to situations of strong water movement than in the British Isles, although the richer, denser growths more frequently occur in those conditions. A summary of its detected occurrence patterns at our sites is presented in Table 1. It will be noted that detected depths in non-turbulent situations require some revision of comments made on the basis of Børgesen's observations. Børgesen (1902: 450) indicated the presence of *A. esculenta* '. . . gregariously in enormous masses from about low-water mark to several fathoms below it . . .', but elsewhere (1905: 754) qualified this by stating that the association preferred steep or vertical rocks in most exposed places, there developing '. . . a dense covering, often many feet thick, at varying but hardly ever very great depths. Yet the *Alaria* may be found at a depth of several fathoms, as in sounds where there is a rapid current . . . [where] *Alaria* is often richly represented in the *Laminaria hyperborea*-association.' It will be clear from profiles presented in the figures and from the summary in Table 1 that this is not wholly supported here. Sound areas with fast currents (e.g. at station 25) certainly carry *Alaria* on bedrock and sufficiently stable boulders to substantial depths. But these circumstances are neither the only conditions in which *Alaria* occurs at such depths, nor indeed the greatest depths at which *Alaria* occurs. An additional qualification rests in the nature of the depth penetration. The requirement for strong water movement does not seem to be a restricting factor in the occurrence of *Alaria* at depths beyond the subtidal fringing band, nor does the penetration of greater depths always occur as a continuous pattern of penetration stretching down from the lower limit of the subtidal fringing populations to the greatest depths achieved. Station 4 (Húsavík, Sandoy), for example, is a comparatively calm area close to a harbour wall where the only induced movement of water at depths results from the effect of the wall itself; that movement is not great. Quite vigorous mixed growths of *Alaria* and *Laminaria saccharina* occurred there to depths of 7 m, with the most dense growths being in the 6–7 m band, clearly separated from the other dense fruiting band on the wall and adjacent boulders at 0–1 m depths. Between the two major growth depths were only irregular straggly plants of *Alaria*.

Another example of discontinuous depth distribution in by no means strongly exposed situations is provided by station 19, the Hoyvík area of detailed transects. There, the peripheral subtidal fringe *Alaria* growths on bedrock gave way to quite dense *L. hyperborea* growths at about 2·5 m depth; *Alaria* re-established itself at greater depths only as a clearly delimited mixed and vigorously fertile population with *Laminaria digitata* on stony and bouldered patches in 5–6 m depths. Even the growths at 2·5 m depth were only a few scattered large but healthy plants amongst *Laminaria hyperborea* on a ledge of favourable configuration; the true subtidal fringe growths terminated without noticeable downcarry well above that, at a few centimetres depth.

Populations in depths beyond the first 2 m often represent only sporelings, as at stations 27 (sporelings over 2–3 m depths) and 44 (a few sporelings at 15 m, the deepest at which we detected this species). Sites with rather stronger water movement had either discontinuous depth distribution of *Alaria* (e.g. station 34), with the main band on steep rock down to *c.*2 m depth and smaller (but still vigorous and mature) clumps in greater depths (often in the shelter of gullies) of some 8–10 m, or a continuous depth distribution with very different vigour at different depths. Stations 29 and 30, both steep rock areas with very strong water movement,

Table 1 *Alaria* on the Faroes.

a. Epilithic

Station	Substrate	Depths (m)	Notes
4	wall	0–1	fertile.
	broken boulders below/away from wall	(1–)6–7	mixed with *Laminaria saccharina*.
5	wall	+0·5 to +0·6	dense band 10 cm deep.
	boulders away from wall	0–4	
12	steep bedrock	1–2	band-forming.
13	steep rocks and irregular large boulders	around ELWS	abundant dense fertile band along subtidal fringe of exposed head; alongside *Ascophyllum* passing into bay.
14	firm rock	0–2	*Audouinella alariae* on blade.
15	rocks and large boulders	around 0	dense fringe along whole slab shore.
18	rocks	0–1	heads and coves: dense narrow fringe in wave-/water-wash; mixed with *Laminaria digitata*.
19	rocky firm areas	+0·2 to 0·2	head profile and comparative cove 2; admixed with *Laminaria digitata* and *Himanthalia*.
	rocky firm areas	2·5	head profile; few scattered large healthy plants amongst *Laminaria hyperborea* on ledge.
	stony/bouldered patches	5–6	comparative cove 1; intermix of well-developed fertile plants with similar *Laminaria digitata*.
20	rocks and firm boulders	around ELWS	band peripheral to pools and shallow subtidal on semi-exposed head; fertile.
23	rocks/boulders	around ELWS	masses forming dense band, fertile sometimes alongside *Ascophyllum*; occasional large rounded plants amongst populations would appear to represent '*Alaria pylaii*'.
24	rocks	0–2	some overlap with *Laminaria hyperborea* below.
25	rocks	1–5	patchy, but luxuriant and dense locally, amongst patches of *Laminaria hyperborea* and *L. faeroensis*; fertile.
27	large broken boulders	0–1(–2)	band-forming.
		2–3	sporelings only.
29	very steep firm rock forming cliff-face	(0–)5–9	1 m overlap with *Laminaria hyperborea* (8–15 m); densest in 5–9 m, where plants also larger; all plants distally tattered.
30	steep rocks and irregular large boulders	(0–)5–10	tattered throughout range; most dense in lower half.
31	steep rocks of very steep to vertical cleft wall	0–1	band-forming.

Table 1 cont.

Station	Substrate	Depths (m)	Notes
34	firm steep to vertical rock	0·5–2	sharp demarcation *Laminaria digitata* (to 0·5 m) to *Alaria* (0·5 m downward): *Alaria* to *Laminaria hyperborea* junction either direct or via young plants of *L. digitata* forming second *digitata* band.
	boulders on gully bottom	8–10	some small clumps in the deeps.
35	small rocks in dark sand	subtidal fringe to 2 m	somewhat patchy; fertile.
36	moderately steep rocks	0–2	patchy, but locally dense band; fertile.
37	steepish firm rock (not boulders)	subtidal fringe to 1 m; to +1 in upcarry areas	band-forming; fertile.
38	steep firm rocks of cleft sides	+0·5 to 0·5	fertile on south (scoured) side.
42	rocks	1–2	band-forming.
44	very large boulders over bedrock, or on other boulders embedded in sand	15	a few sporelings only.

b. Epiphytic

Station	Host	Position	Depths (m)	Notes
11	*Laminaria hyperborea*	stipes	1–2	on few stipes only.

Qualifications
1. Omitted stations lacked recorded data of sufficient precision.
2. All entries relate to *Alaria esculenta* unless notes specify '*A. pylaii*'.
3. Notes concern outstanding characteristics; they do not summarize all available data.
4. All depths are *below* low water unless + sign appears.

revealed continuous *Alaria* growths from the fringe at *c.* 0 m and a little below down to 9 or 10 m. In both cases, the more vigorous and dense growths were in the levels below 5 m depth, plants being tattered even there, probably as a direct result of the strength of water movement.

The effect on distribution where water movement induced by presence or introduction of vertical surfaces results in upcarry of fringe conditions is dramatically demonstrated by Fig. 2, where adjacent natural boulder slopes and harbour (mole) wall are profiled for station 5 (Sandur, Sandoy). Unlike station 4 (see above), water movement at this wall around low water positions remains quite strong and, combined with the verticality of the surface presented for colonization, has resulted in both considerable upcarry of the narrowed but vigorous *Alaria* band and introduction of sponge-associated algal populations (see later).

Laminaria hyperborea and other Laminaria spp.

The *Laminaria hyperborea* forest was a general, but by no means completely consistent, facet of the subtidal flora in both exposed and sheltered open-shore situations. The species itself was represented at least patchily at almost all subtidal sites examined, although there were some exceptions (Table 2). It was not, for example, detected within the sheltered conditions of the

Table 2 *Laminaria hyperborea* on the Faroes.

a. Epilithic

Station	Substrate	Depths range of growth (m)		Plant characteristics	Notes
		(a) at 'forest' density	(b) otherwise		
4	harbour wall (boulders faced with concrete) (1–6 m) broken boulders below (6–10 m) grading to bedrock (*c.*8–10 m)	(1–)8–10	sand below 10 m	No unusual data	Increasing *Dilsea* underflora with depth.
5	concreted vertical wall; boulders below, or alongside (0–7 m on wall; 4–12 m on boulders)	0–12	detritus below 12 m	No unusual data	—
7	firm rock of vertical face; large boulders on easing slope below vertical	9–17	above 9 m	large plants below 9 m	Data incomplete.
9	vertical rock face; boulders below	5–9	? depths below; (1–)5 above	No unusual data	Forest present below 9 m; accurate limits not known.
10	firm rock	5 and down	1–5	No unusual data	Lower limits not known.
11	vertical to very steep rock	1–12	'waifs and strays' to 20 m	No unusual data	—
12	rock and boulders; deeper plants on scattered rocks in/on gravel	10–22	(–30)	30 m—small plants with long stipes/attenuate blades; 25 m—slightly larger, but still scattered; 22 and up—'forest'-sized plants	Forest deeper than seen elsewhere on Faroes.
13	firm rock of irregular, steep to moderately steep, configuration	—	—	—	General data only; depth limits not recorded.

14	harbour wall; irregular rocks below	1–10	detritus below 10 m	No unusual data	Dive limits not deep.
18	firm rock; large boulders	2 and down	not known	No unusual data	Plants breaking water at LWS, 5–10 m offshore.
19 (Head)	gentle bedrock slope; verticals of ledging occasionally steeper	1·5–10+	0·5–1·5	Shallow growths—few small plants amongst barnacles; 1·5 m and down—large plants	Few intermixed large *Alaria* on ledge at 2·5 m.
19 (Coves 1 and 2)	gently sloping firm rock; verticals of traversing ledges	0·5–9	—	Younger and more etiolated than plants off head	Absent from stony and sandy patches.
21	steepish firm rock	1–10	10–24	Smaller plants from 10 m and down	Forest thick above, opening to sparser with depths.
22	steep offshore rock surfaces	1–10	10–20	No unusual data	—
23	firm rock and large boulders	2 and down	not known	—	Few plants below *Laminaria digitata*, off peninsula tip.
24	bedrock and large boulders	1–9	not known	Long thick stipes, small blades	Moderate forest; substrate levelled off at dive limit (9 m); overlap above with *Alaria* due to upcarry in wash.
25	solid bedrock with small boulders	None	1–7	Whitish—Polyzoa covered	Locally scattered intermixed patches of *Alaria*/*L. digitata*.
28	bedrock; sandy patches at intervals	5–7	not known	oldish plants	On bedrock; only these depths available.
29	very steep, firm rock cliff face	None	8–15	plants everywhere isolated, small, scattered; from less than 15 cm (at 15 m) to 30–60 cm (at 8 m)	Some overlap with *Alaria* (0–9 m).
30	steep irregular firm rock and boulders	10–16+	deeper, but lower limit not known	Large plants in forest	Dive terminated in 16 m.
31 (outside cleft)	steep to very steep firm rock face	3–15	grading out over 3–5 m and 12–15 m	Thinning and size reduction over 3–5 m and 12–15 m	Profile outside main cleft, to west.

Table 2 cont.

Station	Substrate	Depths range of growth (m) (a) at 'forest' density	(b) otherwise	Plant characteristics	Notes
31 (outside cleft)	irregular boulder slope, at angle decrease below steep wall	None	*c.*20–22	Small plants throughout	Plants isolated and scattered.
33	rocks outcropping through and boulders/ stones on sand	2–3	no greater depths in fjordic inlet	No unusual data	Standard forest with intrusive gullies.
34	vertical bedrock faces (2–8 m); boulders over detritus (8–16 m); bedrock with sand channels (8–16 m)	(2–)7–16	2–4(–7)	Straggly, small, and sparse (2–3 m); more abundant, denser and bigger by 3–4 m; very large and strong, stipes almost unbreakable by 16 m	Forest density from lower wall (*c.*7 m) to 16 m (in channels in bedrock).
35 (Ánir)	small boulders in dark sand	shallow subtidal, to *c.*2 m	no data	No unusual data	Meadow just offshore.
35 (Dive)	loose detritus of sand/gravel, with boulders and occasional bedrock; *Modiolus* throughout	10 (almost forest, to scattered)	10–20	Decrease in size/ density from 10 to 20 m; sparse, overall small, not usual long stipe by 20 m	—
36	moderately steep firm rock; boulders on detritus below	—	—	—	General observations; no firm additional data.

38	steep firm rock walls of cleft	0·5–6·5 (non-scoured, south, side)	0·5–6·5 (scoured, north, side)	Young example—blade, 30 cm; stipe, 60 cm; Older plants—blade, to 45 cm; stipe, 95 cm	Full cleft depths to firm bottom, 7 m depth.
39	rock	5–7	—	—	Only 5–7 m depths examined.
41	large boulders	1–9	no data	—	Present below 9 m, but density and limits not recorded.
42	steepening firm rock	3 and down	not known	—	Subtidal dominant below, but density and limits not recorded.
44	very large boulders	15–*c.*20	(–29)	attenuation and reduction in size and density with depths	Present above, but detailed data from 15–29 m only.
Langasandur, Sundini	good-sized, but variable, boulders set in mud;	None	(1–)2–4(–5)	mainly f. *cucullata*	Only available substrate 4–5 m, plants occasional.
	bedrock	None	(1–)2–4	mainly f. *cucullata*	Abundant, to 4 m.

b. Epiphytic

Station	Host	Position	Depths (m)
36	*Laminaria hyperborea*	on stipes	5

Qualifications
1. Species either lacking or not recorded from omitted stations (see text for fuller distinctions).
2. Notes do not summarize all available data; important topics are explored further in text.
3. All depths are *below* low water levels.
4. No evidence of growth to maturity as an epiphyte.
5. Langasandur is included as a comparative example of fjordic/sound situations.

harbour at Eiði (station 27), where the large broken boulders grading into blackish shell sand at 9–10 m depths were dominated by a mixed population of *Laminaria saccharina* and *Desmarestia aculeata.* Harbour conditions elsewhere, both in and outside fjords, tended to be dominated in otherwise *L. hyperborea* depths by either *L. saccharina* in various combinations with large algae of other groups, or mixtures in varying proportions of *L. saccharina* and *L. faeroensis** (as, for example, in the artificial harbour on the north shore of Kollafjørður). Elsewhere in Kollafjørður (Jøkilsgjógv, on the steep western shore of Tangafjørður opposite Raktangi—station 23— and at the extreme outer entrance to Kollafjørður), *L. saccharina* and *L. faeroensis* were sufficiently vigorous and dense to form replacement forest, for the more usual dominant *L. hyperborea,* between 1 m and 5–6 m depths. Very large *L. saccharina*/*L. faeroensis* within these depths bore laminae up to 16 ft (*c.*5 m) long. Within fjords but outside harbour conditions, at least some *L. hyperborea* was usually present, often at its 'cape' form (f. *cucullata*); this form occurred in 2–3 m depths at Jøkilsgjógv.

The circumstances in which the open shore presence of *L. hyperborea* did not result in the formation of forest were detected at Station 29 (near Stakkur, north-west Streymoy) and presumably reflected too steep an angle on the cliff face in very turbulent conditions, followed by too mobile a substratum where the angle eased to a boulder-strewn bottom at 23 m. Elsewhere, particularly at station 12 (Nólsoy), distribution depths of forest density of *Laminaria hyperborea* varied quite markedly from the usual situation. Development of forest density commonly occurred on firm but not excessively steep natural substrata between (0–)4–16(–22) m depths. At station 12, forest growth was definitely deeper than anywhere else examined around Faeroese shores, beginning at about 10 m and descending to 22 m and below before thinning to become scattered but still large plants. Small plants with long stipes and attenuate blades were still present attached to scattered rocks amongst the gravel substrate down to 30 m depths. This tallies well with the 15 fathoms maximum depths for the species noted by Børgesen (1905: 758–759), although he elsewhere (1902: 462) commented that the '. . . proper habitat is from a depth of a few to as much as 10 fathoms, sometimes even to almost twice that depth.'

Because it is a relatively larger plant with erect stipe and usually grows in depths greater than such species as *L. digitata, L. saccharina* or *Alaria, Laminaria hyperborea* generally shows less overt and identifiable effects of upcarry by local configuration in its vertical distribution. Nevertheless, it is occasionally possible to identify such effects, as at station 24 (Kvívík) where definite overlap with the *Alaria* band (occupying depths of 0 to 2 m) was promoted by the upcarry of *L. hyperborea* plants in shallow subtidal channels in the bedrock.

The mosaic situation that occurs with the major laminarian bands in some localized areas, even in the absence of substrate variation, is exemplified by data recorded at station 34 (Kalsoyarfjørður, off the west coast of Kunoy). The lower intertidal and shallow subtidal there is generally, down to at least 8 m, a very steep to vertical rock-face; below that, the slope eases and the substrate changes to boulders over detritus, penetrated by sandy channels clear of boulders. Sandy channels persist amongst the bedrock that succeeds the boulders at 16 m. The vertical rock that terminates in about 8 m is cleft in places rather deeply; the inner ends of clefts show erosion caves with basal detrital build-up that submerges the lower 1 metre of the rear and side walls. *Laminaria digitata* formed a fairly consistent one-metre band between 0·5 m above and 0·5 m below the low-water level; it lacked epiphytes and had only straggly *Plocamium* as underflora. Below −0·5 m and sharply demarcated (but not spaced) from *Laminaria digitata* was a band of *Alaria,* occupying −0·5 m to 1(–2) m depths. Small outlying clumps of *Alaria* also occurred on boulders on gully bottoms in 8–10 m depths. The lower limit of the *Alaria* upper band was complex; in places (and this was most common) was a graded but continuous transition from *Alaria* to fully-developed, but straggly and sparse, *Laminaria hyperborea* over the 2–3 m depths band. In other places, young *Laminaria hyperborea* plants occurred between *Alaria* and *Laminaria hyperborea,* mixing into the upper fringe of the latter. The straggly and sparse *L. hyperborea* quickly (by 3–4 m depths) became more abundant, larger and denser, in a continuous sequence to about 8 m, the bottom of the almost vertical wall. By then, true forest

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*A name used for convenience only; see Irvine (1982).

Table 3 Other laminarians on the Faroes

Laminaria saccharina

a. Epilithic

Station	Substrate	Depths (m)	Notes
4	broken boulders (1–10 m) grading to bedrock with stones in sandy gullies (8–10 m)	1–10	mixed with *Alaria,* 1–6 m; plants on stones in sandy gullies at *c.* 10 m often buried to 7–10 cm up stipe.
5	firm boulders	4–12	mixed with *Desmarestia aculeata* and massive *Chaetomorpha melagonium*
13	sheltered positions on rock	shallow subtidal	inside shelter of harbour back from exposed headland.
15	firm rock and boulders	shallow subtidal	only in harbour formed by artificial moles; not on open natural coast.
18	firm rock and boulders	shallow subtidal to 2 m	masses of large plants, mixed with *L. digitata,* in sheltered 'lagoon'.
19	on stony/bouldered patches	5–6	in cove 1 alongside headland; not on fringing bedrock; equal intermix of large fertile *Alaria* and *L. saccharina*.
20	firm rock	all deep pools and shallow subtidal	in semi-exposed positions on head.
24	extensive sand-covered gullies in bedrock	4–6	some on larger fragments and on lateral bedrock.
25	small boulders on solid substrate	1–7	*Laminaria faeroensis*; as locally scattered, patchy mixture in equal proportions with *Alaria* and *Laminaria hyperborea*; with thick stipes and long blades.
27	large broken boulders	1–9	codominant with *Desmarestia aculeata* below *Alaria*.
31	boulders stabilized in sand	*c.* 5–6	common and locally dense; inner end of main cleft.
35 (Ánir)	small boulders in dark sand; concrete artificial substrata	shallow subtidal, to 3–4 m	large vigorous plants; iridescent.
42	shallowly-sloping firm rock, giving way to steeper face	1–2	in sheltered positions; few plants, mixed with *Alaria*.

b. Epiphytic

Station	Host	Position	Depths (m)
36	*Laminaria hyperborea*	on stipes	5

Laminaria digitata

a. Epilithic

Station	Substrate	Depths (m)	Notes
9	steep to vertical firm rock	1–5	above *L. hyperborea* forest.

Table 3 cont.

Station	Substrate	Depths (m)	Notes
13	firm rock of irregular but steepish slope	shallow subtidal	narrow fringe around most of head; more luxuriant into bay to south.
18	firm rock and large boulders	shallow subtidal to 2 m; lower intertidal pools	below or mixed with *Alaria* in exposure; with *Laminaria saccharina* in shelter.
19 (head and cove 2)	steep firm rock	lower intertidal/shallow subtidal, low water ±15 cm, as band of laminarians	few plants admixed in *Alaria* band.
20	firm rock on headland	all deep pools and shallow subtidal	in semi-exposed positions.
23	firm rock and boulders	1–2	good plants, below *Alaria*.
34	firm steep to vertical rock	+0·5 to 0·5	young plants lower, forming interband between *Alaria* and *L. hyperborea*; no epiphytes noted.
35 (Ánir)	some boulders on detritus; also on artificial concrete/ metal/wood quay	subtidal fringe, to 2 m	strong fringe, especially on quay.
36	moderately steep firm rock	lower intertidal pools; shallow subtidal to about 2 m	densely present at about 2 m; above more sporadic, amongst *Alaria* and in pools.
37	steepish firm rock	1–2	exposed shore; firm band below *Alaria*, occasionally above it where *Alaria* patchy; grades to *L. hyperborea*.
38	on steep upper firm rock sides of cleft	mixed with *Alaria* in 0–0·5 m on north (scoured) side of cleft; forming narrow band over 0·33 to 1 m, below *Alaria* (+0·33 to 0·33) on south (non-scoured) side	see depths comments.
42	shallowly-sloping firm rock, giving way to steeper face	2–3; also some intertidal pools	fringing band, patchy, below *Alaria*.

b. Epiphytic

Station	Host	Position	Depths (m)
Lambareidi, Skálafjørður.	*Laminaria faeroensis*	on stipes	shallow subtidal (within 2 m)

Chorda filum

a. Epilithic

Station	Substrate	Depths (m)	Notes
20	firm rock and large boulders	subtidal fringe, to 2 m	in more shaded and wave-sheltered parts; few plants only.

Table 3 cont.

Station	Substrate	Depths (m)	Notes
23	larger fragments in mobile substrate	shallow subtidal, in channel deepening to 1 m	—
Hvannasund (causeway/ lagoon)	boulders on detritus	in deeper parts of lagoon only, *c.* 1–2 m	sheltered by artificial closure by causeway and protection from harbour moles.

Qualifications
1. Omitted stations lack appropriate data.
2. For details of *Alaria* distribution, see Table 1; for *Laminaria hyperborea,* see Table 2.
3. Presence of *Laminaria faeroensis, Alaria,* and *Laminaria hyperborea* far into Sundini (25) derives from fast flow in sheltered sound.
4. Depths are *below* low water unless sign + appears.
5. All *Chorda filum* records from stations sheltered from wave-action.

density being reached, the plants were large and dense; the forest persisted over boulders and in bedrock channels to the limit (16 m) of the dive, by which depth *L. hyperborea* plants were very large and strong, with unbreakable stipes, and the forest was very dense. Although the *Laminaria hyperborea* forest was by no means devoid of underflora (see station profile and the appropriate later section), stipe epiphytes were the more obvious subordinate flora in the upper 4–5 m of the *Laminaria hyperborea* depths; richer and more dense underflora developed in thinning areas and with increasing depths, although the boulders over detritus in 8–16 m depths showed very few of the usually very obvious crusts (e.g. of *Cruoria, Pseudolithoderma,* Lithothamnia), probably due to canopy outshading (see Discussion and conclusions for detailed comment).

Where slightly more sheltered locations produced conditions that would also support growths, at least locally, of *Laminaria saccharina,* as at Ánir (Haraldssund, station 35), fairly strong mosaic intermixing of all four of the more common 'open shore' laminarians occurred. Ánir has an intermittently strong throughflow of water just off-shore, but this hardly directly affects the shore-wise conditions in the subtidal of the boathouse-and-quays area examined. There, and immediately offshore, juxtapositions of *Laminaria hyperborea* ('forest' to 2 m in the shallow subtidal, on small boulders buried in dark sand); *Alaria* (the usual fringe on same substrate and in same depths as *L. hyperborea*, but locally patchy only); *Laminaria digitata* (strong fringing growths at and just below extreme low water mark of spring tides on the artificial substrata of the quay, concrete, metal and wood; some plants on boulders in the detritus); *Laminaria saccharina* (principally on small boulders in the dark sand in shallow subtidal depths to 3–4 m; some specimens present on concrete artificial substrata at the water level), are impressive if irregular. Similar mosaic juxtaposing of all four common species was noted at stations 13; 18; 19; 23 (the latter with *Chorda filum* substituted for *L. saccharina*); and 42. The numbers of instances where three of the four species were juxtaposed, the missing fourth usually being either *L. saccharina* or *L. digitata,* are legion (see Tables 1, 2, 3).

Open shore populations of *Laminaria saccharina* are in our experience rarely present in considerable depths, although Jóhansen (1979) gave limits on the Faroes as in 10–15 m. This shallow growth was at least in part due to the fact that along open shores the appropriate sheltered water conditions most frequently occur in protected channels, coves and inlets, where available depths are shallow. Reference to Table 3 will show that only at two stations (4 and 5), both with a high degree of extra protection from adjacent harbour walls in already wave-sheltered conditions, was *L. saccharina* detected at 10 m depth or greater. Similarly at Eiði (station 27), where the species was detected down to 9 m, harbour conditions were again involved. Maximum depths otherwise noted were, according to local configuration, 6–7 m, and most populations grew within the first 5 m. Depth limits of the more exposure-tolerant *Laminaria digitata* were even more rigorous; the great majority of observed populations grew within the narrow fringe covered by the first 2 m depth. Only a few plants in the growths at stations 9 and 42 attained the 5 m and 3 m depths respectively detected as maxima. Jóhansen (1979), however, recorded 10–15 m depths for Faroese *L. digitata. Chorda filum* was noted in very shallow fringe conditions only, but in too few instances for assessment on a general basis, particularly in view of Jóhansen's (1979) statement of 1–10 m as the depth range.

All *Laminaria hyperborea* populations, of forest density or not, showed with increasing depths an increase in density and luxuriance up to a maximum that occurs most commonly between 4 and 12 m, and a subsequent decrease in such parameters that occurs over a greater depth range than did the initial increase, usually 8 m or so against 2 m or so (Table 2). This negatively skewed density curve is more or less paralleled, although with the individual size of plants somewhat more positively skewed, by curves of plant size and epiphyte density. This latter is also more positively skewed, but less so than is plant size. Variation in plant size between average in the densest depth range and average in the sparsest depth range can be quite impressive—absolute measures between largest and smallest even more so. Even at station 29 (near Stakkur), where plants were relatively poorly-developed and forest density was not formed at any depths, plants at the upper limits of *L. hyperborea* growth (8 m depth) were up to 60 cm total length, whilst at the lower limits (15 m), total lengths were less than 15 cm. In populations more representative of full potential development, similar proportional growth and characteristics are revealed, but plant and density dimensions are very much greater.

Size reduction from the optimal depths range at a particular location is usually manifest as a reduction in blade size and a thinning and shortening of the stipe, especially where the plants are growing in more shallow depths. Similar changes will very often be apparent between optimal growths present at favourable locations and those at adjacent less favourable ones as, for example, at station 19 (Hoyvík transects), where plants off to seaward of the head were much larger and more robust than the small etiolated ones (with smaller blades and thinner stipes) representing optimum growths in the adjacent cove to the south. Reduction in stipe length is often not manifest with increasing depth below the lower fringe of forest density growth. Indeed, plants below the forest will often have even longer stipes than in optimal conditions; in Faroese populations observed (e.g. at station 12) such plants always possessed markedly *thinner* stipes than did those from the forest depths. In forest depths, plants often had long thick stipes and relatively small or attenuate blades (for example at station 24), although this is not always so since blade size increase over adjacent less favourable greater or lesser depths may be in the same proportion as stipe augmentation (as at stations 30 and 34). Station 34 (west Kunoy) perhaps best exemplifies the idealized sequence of changing size and proportion of *Laminaria hyperborea* growth with depth (see profile, Fig. 8). Locally variable in shallow depths according to shoreline and substrate configuration, plants most usually were straggly and sparse below *Alaria* at about 2 m depth. At around 3 m depth (although in places not until 4 or 5 m depth), there ensued considerable rapid increase in abundance, size and density over the depths (3–)4–8 m, the latter usually being the optimum for all characteristics. Not much change thenceforth to 16 m was noted, plants at this latter depth being very large and strong, with virtually unbreakable stipes. Substrate changes over forest depths from about 5 to 16 m, from very steep or vertical rock (to 8 m), followed by rock channels or gullies amongst large boulders on detritus, giving way in turn at about 12 m or so to smaller boulders more closely arranged, with bedrock tongues and sandy channels coming in at 16 m, may well have contributed to slight thinning of forest density at about the 16 m depth, the limit of the detailed dive. More casual observations below that indicated more marked thinning with increasing depth.

The effects of artificial available substrata on this usual growth and distribution pattern were noted at a few locations; harbour walls, moles and quays were the most important constructions. The most common overall effect was an increase in homogeneity of growth size and density over the available depth range of artificial substrate. A narrower higher *Alaria* band giving way much more quickly to dense *L. hyperborea* growths than occurred on adjacent boulders at similar depths away from the harbour wall was also usual, as at station 5 (Sandur, Sandoy; see profile, Fig. 2). Concomitant changes in the pattern of under- and epiphytic flora and fauna are clearly shown by the profile and are treated in detail later; the steep to vertical nature of the substrate and the wash-patterns created probably are also implicated in such changes, since some similar characteristics are manifest on the very steep sides of the outer cleft at Gjógv (station 31; Fig. 7).

Populations at depths greater than laminarian limits

Considerable amounts of previous descriptive literature on eastern Atlantic subtidal depth-distribution of organisms indicate algal populations often characterized below laminarian limits by variably-constituted assemblages of principally filamentous red algae. No such assemblages were detected in any of the subtidal stations examined in detail on the Faroes. Certain red filamentous forms are luxuriant and widespread in lesser depths and in other conditions, but these play little or no part in characterizing the deeper populations. *Pterosiphonia parasitica, Ceramium rubrum, Audouinella purpurea, Polysiphonia urceolata, Ptilota serrata,* and *P. plumosa*, as examples, are all of importance in subtidal situations, but it will be clear from the profiles and other data presented that they do not occur as assemblages of the kind concerned. Distributional characteristics of all detected ecologically significant individual species (other than major laminarians and fucoids) are summarized in Table 4.

Although *Polysiphonia urceolata* was occasionally (as at stations 12, 22, 35 and 44) detected as substantial tufts on rocks and horizontal surfaces of boulders in detritus or on bedrock, algal populations below the lower limits of significant laminarian growth were commonly characterized by crustose growths, of which the major constituents were *Cruoria pellita, Pseudolithoderma extensum,* and the Lithothamnia (especially *Lithothamnion glaciale* and *Leptophytum laeve*). Locally dense clumps of certain other erect forms occurred on rocks, stones, or boulders at considerable depths. Such clumps never obscured the characterizing contribution by the crusts mentioned. Most widespread erect forms were the species *Dilsea carnosa, Delesseria sanguinea* (also recorded in Jóhansen, 1979, as between 10 and 40 m depths), *Callophyllis lacinata, Membranoptera alata, Ptilota serrata, Phycodrys rubens,* and *Plocamium cartilagineum/Callophyllis cristata* (station 12), *Odonthalia dentata* (station 44), and *Phyllophora crispa* (station 35) were less often noted in depths greater than 20 m, although *Odonthalia dentata* has been recorded (in Jóhansen, 1979) at between 10 and 25 m depths. Not all erect growths that occurred amongst the deeper populations of marine algae were Rhodophyta. *Desmarestia aculeata* (stations 11, 21, 22, 31, 44) and, less often, *Desmarestia viridis* (stations 22, 44) were frequently noted, but only infrequently fully below the limits of the *Laminaria hyperborea* populations at the same localities. Similarly rarely appearing below the thinning lower areas of *L. hyperborea* growth were *Ulva lactuca* (station 44), *Fimbrifolium dichotomum* (station 12), and *Corallina officinalis* (stations 29, 31). Rare species such as *Brongniartella byssoides* (station 44) occasionally occurred in open spaces nearing the *L. hyperborea* limits.

It should be clearly noted that none of the species referred to above demonstrated restriction to these greater depths. All occurred in much shallower subtidal situations; as epiphytes on *Laminaria hyperborea* and/or other larger species; in shaded pools within the lower intertidal levels of the shore; or in combinations of these other circumstances. Detailed treatments of these other occurrences are presented in other sections and the habitat tolerance limits of individual species are summarized in Table 4.

ii. Subtidal: epiphytes and underflora

There is everywhere considerable similarity in major constituent species of the underflora and epiphytic flora associated with the *Laminaria hyperborea* forest and its upper/lower fringes (Price & Tittley, 1978; Hiscock & Mitchell, 1980). This is also true for a comparison of *either* flora, (a) with erect and crustose species growing *below* the laminarian limits; (b) with species associated with *Alaria/L. saccharina/L. digitata* levels; (c) with that of shaded lower-shore pools manifesting subtidal upcarry. Rather specialized habitats such as epizoic growth, or vertical to

[*Text continued on p. 211.*]

Table 4 A summary of data recorded for epilithic, epizoic, and epiphytic subordinate flora.

Species	Total epilithic stations recorded (1)	Substrate types	Epilithic depth range (m)	Total epizoic/ epiphytic stations recorded (2)	Host plants/ animals	Position on host	Depth range on host (m)	Overall depth range characteristics	Notes
'Aglaozonia parvula'	—	—	—	2	*Laminaria hyperborea*	bases (stipes; haptera)	shallow ST, 0–?10.	as epiphytic; data sparse.	*New records;* epiphytic stage of erect epilithic *Cutleria.*
Antithamnion floccosum	3	concrete facing of slab walls; polythene bristles; stabilized stones and small boulders.	ELWS to 2 m.	2	on 'Aglaozonia', itself on *L. hyperborea*	surface	(1–)2–?10.	ELWS (IT); 0–*c.*10 (ST). Locally ELWS band-forming, on rock.	⊕, ♂, ♀, ♀ (all at 16B); mostly in fjords or harbours; very small amounts on 'Aglaozonia'.
Antithamnion plumula (var. *demersum* of L 'Hardy-Halos)	2	ledges in vertical rock; tops of large boulders.	10–15.	—	—	—	—	as epilithic range.	⊕; less often ♂; never dense, but locally well-represented; usually away from strong water-movement.
Asperococcus fistulosus	—	—	—	3	*Fucus vesiculosus* *F. spiralis* *F. distichus* *Gigartina stellata* *Laminaria saccharina* *L. faeroensis*	laminae laminae laminae distal stipes; laminae stipes; laminae	as overall.	mid to low IT pools and wet; shallow ST in sheltered harbours.	often only small amounts locally.
Asperococcus turneri	1	stabilized stones in/on detritus.	as overall.	1	*Desmarestia aculeata*	distal on old plants	as overall.	ST: 6–7 m in shelter.	locally few plants in few locations.
Audouinella alariae	—	—	—	2	*Alaria esculenta*	laminae	fringe to 2 m.	as epiphytic.	rare, but locally luxuriant on individual laminae.

Audouinella daviesii	—	—	—	3	*Palmaria palmata* *Cladophora sericea*	blades distal	LWS to shallow ST.	LWS to shallow ST.	probably more widespread than recorded; *Palmaria* host on *Laminaria hyperborea* stipes.
Audouinella purpurea	6	firm rock; walls; stabilized stones.	spray zone to lower IT.	2	*Laminaria hyperborea*	stipes	0–5.	continuous, adding **(1)** to **(2)**.	some on walls of ruined Kirkjubøur cathedral; in caves; turf usually luxuriant where present.
Audouinella secundata	—	—	—	6	*Phycodrys rubens* *Ceramium rubrum* *Callithamnion sepositum* *Pilayella littoralis* *Ectocarpus fasciculatus* esp. Ceramiaceae	young only — — — — —	mid IT to 3 (ST).	mid IT pools/ wet, to 3 m.	more widespread than recorded; terminal hairs occasional (16B); dense branching occasional (15).
Audouinella spetsbergensis (penicilliforme)	—	—	—	1	*Lomentaria orcadensis*	—	lower IT/ ST fringe, in exposure.	as epiphytic.	well-developed plates present; probably more widespread.
Audouinella virgatula	—	—	—	3	*Porphyra umbilicalis* *Ceramium rubrum* various other spp.	— — —	top shore to lower IT; shallow ST.	as epiphytic.	probably more widespread than recorded; 1-layered at base (15).
Audouinella spp.	—	—	—	7	*Plocamium cartilagineum* *Ceramium shuttleworthianum* *Cladophora sericea* and *rupestris* *Callithamnion sepositum* *Enteromorpha compressa* *Antithamnion floccosum*	tips — — — — —	mid to lower IT; shallow ST.	as epiphytic.	massive sporangial growths on *E. compressa* (16B); more than one undetermined species involved in these records.

Table 4 cont.

Bangia atropurpurea	2	firm steep rock; large stable boulders, often in overhangs/ shade.	upper mid IT, in wet/ wavewash.	1	*Fucus distichus* (also enmeshed with *Ulothrix*/ *Urospora*)	laminae	lower IT in wet/ wave-wash.	upper mid IT (as band) to lower IT (epiphytic) in wet/wave-wash.	continuous locally as band-former, above/ mixed with *Palmaria*; withstands constant freshwater downwash (26).
Blidingia minima	13	firm rock; large stable boulders; concrete slipways/harbour walls.	top shore at *Pelvetia*/ *Prasiola* level; also in pools.	1	barnacles	shells	top shore at *Porphyra umbilicalis* level.	irregularly to continuous band-forming, top shore and in upper shore pools.	slightly lower on shore when epizoic (19).
Brongniartella byssoides	3	firm rock, vertical to horizontal; large boulders.	ST: 3–5; 10–15; *c.*20.	—	—	—	—	discontinuous in ST; depths as given in epilithic entry.	uncommon; usually in clefts or open spaces; few plants only (respectively 3; 2–3; 5).
Bryopsis plumosa	3	firm rock or large stable boulders.	lower IT to MTL, pools and wet overhangs; ST on horizontal rock, 10–15 m.	—	—	—	—	as epilithic; IT mostly in shade or wet deeps; patchily discontinuous.	swards in deeper MTL pools, usually in reduced light; 2 plants only found in ST.
Callophyllis cristata	20	firm rock; boulders on detritus or on bedrock; concrete facing to harbour walls; sometimes sponge-associated.	IT pools; ST (0–)1–20(–25).	15	*Laminaria hyperborea* *Palmaria palmata* *Gibbula* barnacles *Halichondria*	holdfasts; stipe bases (less often higher) shells shells associated with	IT tide pools; splash zone with *Palmaria*; low IT in wet; to 25+ m (1–20 mostly).	mostly continuous; sometimes stepwise due to conditions (30: present above on wall; absent 7–10 m; present below in forest).	♀ at 6 stations (**2**); ♀ at 8 stations (**1**); often as both underflora and epiphyte to *Laminaria hyperborea*; small, much-dissected in IT.

Callophyllis lacinata	21	firm rock; boulders; stones in/on gravel and detritus; concrete facing of harbour walls; verticals with sponges (rare).	0–30	10	*Laminaria hyperborea*	stipes (rarely on laminae and holdfasts).	1–22+.	often best developed in middle depths (5–15 m).	mostly with *Callocolax*, although latter patchy; often more epilithic than epiphytic, when present together; epilithic plants in depths (as e.g. at 29) sometimes small and rosetted.
Ceramium diaphanum	1	rocks and boulders.	Lower IT and shallow ST.	1	*Laminaria saccharina*	laminae	lower IT and shallow ST.	continuous over narrow amplitude.	detected only in Torshavn area and adjacent fjords as· *new records;* not abundant but possibly more widespread; epilithic plants with ⊕ and ♂.
					L. faeroensis	laminae			
					Fucus spiralis	laminae			
					F. vesiculosus	laminae			
Ceramium rubrum	11	rocks and boulders	upper mid to low IT in wet; ST 0–9.	11	*Laminaria hyperborea*	stipes and laminae	ST: 5–7.	continuous through depth range (upper mid IT to ST 16 m); always in wet places.	ST 4–8 m; cosmopolitan to the island group; very common as both epiphyte and underflora.
					Corallina officinalis	distal	mid to low IT; pools and wet.		
					Fucus vesiculosus	laminae			
					Ascophyllum	laminae			
					other fucoids	laminae			
					Polysiphonia lanosa	distal			
					Furcellaria lumbricalis	distal	ST: 7–16, in sandy conditions.		
Ceramium shuttleworthianum	15	shallow to steep firm rock and boulders; artificial wall facings.	upper to mid IT draining surfaces; less often lower IT.	1	*Corallina officinalis*	distal	mid IT pools and wet.	continuous over narrow amplitude.	probably more abundant and widespread than even recorded; vast swards at some sites (e.g. 32).

Table 4 cont.

Chaetomorpha capillaris	5	pools in firm rocks/boulders.	IT: upper to lower, in pools. ST: shallow, where water-movement small.	See comments in Notes column			probably locally patchy to dense.	epilithic/epiphytic status doubtful; usually wrapped around *Enteromorpha*/*Corallina* as skeins; sometimes floating free.
Chaetomorpha melagonium	10	firm rock; stones in sandy gullies; firm boulders; artificial concrete slipways.	see overall range column.	4	*Laminaria hyperborea* *Modiolus modiolus*	stipes, especially lower, sometimes throughout shells	see overall range column.	locally patchy to stepwise, due to environmental conditions; in shaded deep pools at all IT levels; ST 0–15 m.	epiphytic growths dense and massive, possibly due blanket population effect since alongside epilithic plants; ‘meadows’ or ‘forests’ on stipes and on rock; deepest as epiphyte, but usually with locally patchy *Desmarestia* in underflora.
Chlorochytrium cohnii	—	—	—	1	naviculoid tubes	—	mid to lower IT.	as epiphytic range column; data inadequate.	fertile; probably more widespread.
Chlorochytrium inclusum	—	—	—	1	*Dilsea carnosa*	widespread and abundant in host.	lower IT; deep shaded undercut pools.	as epiphytic range column; data inadequate.	probably more widespread.
Chlorochytrium sp.	—	—	—	1	*Devaleraea ramentacea*	—	shallow ST lagoon and mole; in 15 cm to 1 m of water.	as epiphytic range column; data inadequate.	probably throughout *Devaleraea* populations.
Chondrus crispus	5	firm rock; boulders; stones in sandy gullies.	IT, in shaded wet lower parts or standing waters; ST 4–6.	—	—	—	—	locally continuous but patchy; detail as epilithic range column.	mostly open rock flora; sometimes few plants; iridescent at sites 20, 23; records from 24, in 4–6 m depths, were of the much-branched form, not the usual ST form.

Chordaria flagelliformis	1	firm rock; boulders.	low IT wet places or standing waters.	3	*Fucus spiralis* *F. distichus* *F. vesiculosus* *Laminaria saccharina* *L. faeroensis* *Gigartina stellata*	laminae laminae laminae laminae laminae distal	lower IT pools and wet; ST (mostly), fringe and shallows.	locally continuous over vertical range.	usually epiphytic; occasionally in small artificial harbours, as large plants (e.g. at 20).
Choreocolax polysiphoniae	—	—	—	2	*Polysiphonia lanosa* (itself on *Ascophyllum*)	median and distal	mid IT, in shelter.	band, delimited by 'host' distribution.	rarely detected; probably more widespread in shelter than recorded.
Cladophora rupestris	10	washed/wet firm rock; boulders on rock or detritus, stabilized; stones in detritus; artificial concrete facings.	mid to low IT in wet, standing water, or pools; ST, to 2 m.	—	—	—	—	continuous vertically; locally dense but patchy horizontally.	often mixed with *Ulva*, and sometimes bearing *Audouinella*; underflora to *Alaria*, *Laminaria digitata* and *Fucus vesiculosus* (in upcarry).
Cladophora sericea	5	firm rock; large boulders; stones in detritus; artificial concrete facings.	mid to lower IT in wet, pools or standing water; not detected below ST fringe.	—	—	—	—	locally dense, but patchy, in IT.	often mixed with *Ulva*, as pool underflora or wet rock flora; more often bearing *Audouinella* than does *Cladophora rupestris*.
Corallina officinalis	17	firm rock; boulders; stabilized stones.	mid to lower IT pools and wet areas; ST, 0–20.	1	*Laminaria hyperborea*	holdfast	ST, 0–5 (site 10).	continuous in IT; locally stepwise in ST— 0–10 continuous 10–18 usually absent 18–20 sporadic.	single clump at 20 m (31) on easing slope; probably more widespread and locally very abundant in IT/ST fringe; small and rare as *L. hyperborea* underflora unless forest open.

Table 4 cont.

Cruoria pellita	14	firm rock; stones and boulders stabilized in sand/gravel; large boulders on rock.	(3–)5–30 (–40).	2	*Laminaria hyperborea* *Modiolus modiolus* *Cyprina islandica* *Lithothamnion glaciale*	stipes shells shells on 'hedgehogs'	ST, 10–15(36) 4–10(23).	continuous locally, but depths vary with site; other data as range entries.	cover often decreases with depths over range; grows most shallowly in least water movement; exceptionally, extensive crusts at depths (44); mostly amongst/under *Laminaria hyperborea* canopy, in spaces; usually admixed with *L. glaciale* and *Pseudolithoderma*.
Cryptopleura ramosa	4	firm rock; large stabilized boulders.	lower IT and fringe in standing water; ST, 5–7.	—	—	—	—	locally discontinuous; other data as range entries.	IT records (Hvítanes) of small amounts of prostrate plants near in form to '*Acrosorium reptans*'; ST records often from steep to vertical rocks, otherwise as *Laminaria hyperborea* underflora.
Cystoclonium purpureum	1	firm rock; large boulders.	lower IT fringe; shaded standing water.	—	—	—	—	as epilithic range column; data inadequate.	much material where found; possibly more widespread, but not overlooked at sites studied.
Delesseria sanguinea	18	firm rock; boulders on bedrock/detritus; concrete facing of harbour walls; stones stabilized in detritus.	lower IT pools and channels, especially in shade; ST, fringe and (0–)1–20(–30) m.	5	*Laminaria hyperborea*	stipes	ST, 1–15.	locally continuous over wide amplitude; occasionally discontinuous due to substrate variations.	fewer plants and larger individuals as *L. hyperborea* epiphyte with depths increase; plants in IT shaded water smaller than average; most abundant and largest plants in 5–16+ m; species extends below forest depths as epilithic growth.

Derbesia marina (cf. *Halicystis*)	See comments in Notes column			8	on or associated with sponges (*Halichondria*; orange finger sponges; dead man's finger sponges), on vertical rock walls, stable boulders in depths on detritus, concrete-faced harbour walls. *Corallina officinalis*	outer surfaces of sponges distally on sponge-associated plants	ST, vertical rock with sponges, 0–15 m; sponge-associated on boulders, in detritus, 18–20 m; on sponge-associated *Corallina* in 2–10 m.	discontinuous due to conditions; see entries in epiphytic/ epizoic range column.	epizoic/epilithic, animal-associated/ epiphytic; often amongst/under *L. hyperborea*; status debatable—not clear whether first on animal or on rock; often few to rare tufts, much material in 5–7 m at 30.
Dermatolithon corallinae	—	—	—	4	*Corallina officinalis*	distal	wet lower IT and shallow ST.	locally patchy; range as in epiphytic column.	probably more widespread than recorded.
Dermatolithon pustulatum	—	—	—	6	*Laminaria hyperborea* *Gigartina stellata* *Furcellaria lumbricalis*	stipes distal distal	lower wet IT; ST, shallow, to 7 m.	abundant and widespread, but locally patchy.	—
Dermatolithon/ *Fosliella*	—	—	—	7	*Laminaria hyperborea* *Gigartina stellata*	stipes distal	IT, lower wave-exposed; ST, 0–7.	locally patchy, but probably more or less continuous.	probably very widespread on the named hosts; characteristically on *Gigartina* (at 5 stations).
Desmarestia aculeata	23	firm rock; large stable boulders on bedrock/ detritus; small stones over solid bedrock; tolerates vertical or horizontal surfaces.	(0–)1–20 (–29).	—	—	—	—	often continuous over local range; once (44) continuous over considerable depth; at 31, showing stepwise absence due to distribution in (12–15 m) or out (21–22+ m) of cleft.	often very large plants as underflora amongst opening kelp, hence size increase as forest thins with depth; sometimes bears *Porphyropsis* (36); codominant with *Laminaria saccharina* in 1–9 m (27); only one to few plants present; deeper growth than *L. hyperborea* (31).

Table 4 cont.

Desmarestia ligulata	1	vertical rock face.	shallow ST, 10–12 m range.	—	—	—	—	data inadequate for assessment.	sporadic, mostly drift, as listed by Børgesen; found moderately frequently by Rex; single plant at Stakkur in 1980.
Desmarestia viridis	19	firm rock, vertical or horizontal; stable boulders on bedrock/ detritus; concrete facing of harbour walls.	(0–)1–15 (–29).	1	*Laminaria hyperborea*	stipes	ST, in main forest at 5–10 m.	maximum in 5–15 m; often localized as band to depths (see Notes); a few rare cases patchily but evenly at all depths (e.g. 44).	clumps larger when in spaces or under open *L. hyperborea* at lower levels; sometimes masses along LWS fringe (23); sometimes absent from *Alaria* levels (30).
Devaleraea (Halosaccion) ramentacea	2	small boulders in sand, or larger ones on bedrock/ detritus.	wet lower IT to shallow ST, to 1 m depth.	—	—	—	—	probably locally continuous over vertical bandwidth, but horizontally patchy according to conditions.	epilithic open, not usually under-flora; probably more widespread than recorded (cf. Børgesen); abundant and luxuriant locally; see *J. mar. biol. Ass. U.K.* **62**:3 (1982)
Dictyosiphon ?chordaria	1	rock surfaces.	shallow standing water at ST fringe.	—	—	—	—	see epilithic range column.	in river estuary at fjord head; single location with plants requiring further confirmation; cold and murky waters.
Dictyosiphon foeniculaceus	2	stable rock surfaces.	see overall range column.	3	*Chordaria flagelliformis* *Fucus spiralis* *F. vesiculosus* *Laminaria digitata* *L. saccharina* *L. faeroensis*	stipes laminae stipes/ laminae stipes stipes stipes	see overall range column.	locally continuous, lower IT pools and wet rock, ST fringe and (mostly) shallow depths.	predominantly in fjords, enclaves and sounds; few plants only at some locations; usually in turbid waters (e.g. harbours) fertile (unilocular sporangia) sometimes.

Dilsea carnosa	21	firm rock; large boulders; latter also stabilized in/on detritus; stones in sand.	lower IT in deep shaded pools; ST, 0–20(–30).	—	—	—	—	locally more or less continuous; details, see epilithic range column.	as underflora to *L. hyperborea*; smaller in deep shade under forest, larger in spaces; locally dense clumps at 30 m, but species tends to grade off with deeper water; fringe under *Alaria*/*Laminaria digitata*.
Dumontia contorta (with *Ulonema rhizophorum*)	3	firm rock of shallow to moderate slope.	MTL to ELWS, pools and wet places.	—	—	—	—	continuous, where present.	⊕ at 42; occasionally dominant on flat surfaces; *Ulonema* (with unilocular sporangia) frequent to consistent.
Ectocarpus fasciculatus	4	firm rock; large broken boulders; boulders/stones over detrital bottoms.	see overall range column.	4	*Himanthalia elongata* *Corallina officinalis* *Asperococcus fistulosus* *Laminaria faeroensis* *Fucus spiralis* *F. vesiculosus* *F. distichus* limpets	thongs distal distal laminae laminae laminae laminae shells	see overall range column.	patchy, horizontally and vertically; in upcarry grooves, mid to lower IT pools and standing waters; ST fringe; ST epilithic/ epiphytic in fjords/harbours, in 0–5/6 m; ST on large boulders in open, 1–9 m.	equally epiphytic or epilithic, less often epizoic; some epilithic material bearing *Audouinella*.
Ectocarpus siliculosus	—	—	—	5	*Callithamnion sepositum* *Asperococcus fistulosus* *Laminaria faeroensis* *Ceramium rubrum*	distal throughout laminae distal	pools and wet lower. half of IT and ST fringes; ST, to 5 m.	see epiphytic range column.	plurilocular sporangia present at 31; often growing in shelter of small harbours/coves.

Table 4 cont.

ectocarpoids, undetermined.	—	—	—	1	*Alaria esculenta*	laminae	ST, shallows in 0–9 m.	as epiphytic range column.	material not traced for determination.
Elachista fucicola	—	—	—	5	*Fucus spiralis* *F. vesiculosus* *F. distichus (anceps)*	laminae laminae laminae	IT; shallow ST.	continuous where locally dense.	fruiting not observed
Elachista scutulata	—	—	—	3	*Himanthalia elongata*	thongs only	lower IT; ST fringe.	continuous where locally dense.	sometimes common and abundant.
Enteromorpha intestinalis	16	firm rock; stable large boulders on detritus/ bedrock; stones in detritus; concrete and concrete-faced artificial surfaces.	see overall depth range column.	1	*Fucus spiralis* *F. vesiculosus* *Laminaria saccharina* *L. faeroensis* barnacles (amongst *Porphyra*)	lamina tips lamina tips stipes; laminae stipes; laminae shells	see overall range column.	probably mostly continuous, at least locally, upper to lower IT pools and wet places; ST fringe and shallow ST, 0–2 m.	very locally dense as epiphyte; more often detected epilithic; fertile at 15; masses in IT standing water, often as more or less pure stands (18; 23); tolerates freshwater downwash (23; 26); ST plants often large (35), especially in shelter (e.g. 4; Hvannasund; both being harbours).
Enteromorpha linza	5	firm rock; large stabilized boulders/stones on bedrock/ detritus.	mid to lower IT, usually in wet or in standing water, in shade and/ or shelter; ST fringe and shallows to 20 m depth.	—	—	—	—	probably vertically continuous, but always locally patchy; detail, see epilithic range column.	often as mixed *Ulva lactuca*/*E. linza* swards in standing water, locally good large material (35).
Enteromorpha torta	—	—	—	1	*Laminaria faeroensis*	holdfast scrapings	shallow ST, 3–4 m.	inadequate data.	*new record for Faroes*; mixed with *Rhizoclonium*; *Polysiphonia urceolata*; *Erythrotrichia carnea*.
Entophysalis conferta	—	—	—	2	*Polysiphonia lanosa*	—	MTL in shelter.	inadequate data; detail, see epiphytic range column.	rarely and restrictedly detected; ? distribution.

Erythrotrichia boryana	—	—	—	1	*Desmarestia aculeata*	old plants	ST, in 7 m.	inadequate data for assessment.	fjordic records only detected.
Erythrotrichia carnea	1	stable small stones/ boulders.	see overall range column.	2	*Laminaria faeroensis* *Asperococcus fistulosus*	holdfast scrapings along whole plant	see overall range column.	shallow ST, in 1–2 m; other data not adequate for assessment.	only detected plants all fjordic; epilithic plants mixed with *Ulva lactuca* bearing *Myrionema*.
Eudesme virescens	2	firm rock; large boulders.	lower IT pools and standing water.	—	—	—	—	data inadequate for assessment; detail, see epilithic range column.	probably widespread in sheltered fjordic conditions.
Fimbrifolium (Rhodophyllis) dichotomum	2	stones in detritus.	within 10 m and 20–30 m depths (ST).	4	*Laminaria hyperborea* *L. digitata* *Ptilota* spp.	stipes holdfasts distal	ST, depths varying with site (0–1; 2–15; 10–20 m, respect.)	inadequate data for clear assessment; masses at 15 m (36).	locally abundant, but sporadic; commonly as *L. hyperborea* epiphyte but small plants on *Ptilota* in depths, with young plants epilithic; see Hansen, 1980, for nomenclatural study.
Fosliella	—	—	—	—	—	—	—	—	see general entry for *Dermatolithon*.
Giffordia sp. *Giffordia granulosa* *Giffordia hincksiae*		see Notes column		3	*Laminaria digitata*	apex of old stipe remains	see overall range column.	ST fringe in shallow inwash semi-exposed area; ST to 5 m; data inadequate for general assessment.	records grouped since few established; plants from Eidi (27) may have been epilithic on gravel in 5 m, origin confused.
Gigartina stellata	16	firm rock; large stable boulders; concrete-faced harbour wall.	wet lower IT; sometimes band from MTL down in upwash areas; pools in low IT; ST to 2 m depth.	?1	Lithothamnia	calcareous surface	ST fringe.	see epilithic range column; locally continuous; very abundant, luxuriant and widespread.	not clear whether calcareous surface of Lithothamnia really constitutes stone (as is probable) from substrate viewpoint; withstands freshwater downwash; even more widespread than here recorded; epiphytic *Dermatolithon*/ *Fosliella* very frequent; plant usually ♀.

Table 4 cont.

Griffithsia flosculosa	1	firm rocks and boulders.	lower IT in pools.	—	—	—	—	inadequate data for assessment.	grouped where present, but sparse material.
Halicystic ovalis (stage of *Derbesia marina*)	—	—	—	2	*Corallina officinalis* Lithothamnia, associated with sponges.	distal surface	IT, shaded pools ⅔ to 1 m above LW; ST, 2–10 m on very steep to vertical walls in cleft.	inadequate data for assessment.	on *Corallina* at both recorded stations; locally more common on Lithothamnia at 31; 13 plants at station 3; see also *Derbesia* entry.
Harveyella mirabilis	—	—	—	1	*Rhodomela confervoides*	distal	wet lower IT.		single recording from Sundini; probably more widespread but not common; ⊕ material.
Hildenbrandia rubra	3	firm rock; stones in mud; boulders.	up to high IT (4 m above water level) on wet rock in caves; shaded IT in wet; ST to 5 m, in fjords.	—	—	—	—	locally discontinuous due to conditions.	locally widespread and frequent on exposed IT; not often detected; ⊕ in ST.
Isthmoplea sphaerophora	—	—	—	3	*Callithamnion sepositum* *C. hookeri* *Gigartina stellata*	mixed with and growing on	mid to lower IT.	inadequate data; probably consistently present with *C. sepositum.*	probably much more widespread than recorded; epiphytic status debatable—no immediate evidence of actual attachment; consistently sporangial.

Leathesia difformis	—	—	—	2	*Corallina officinalis*	distal	mid to lower IT, pools and wet places.	inadequate data.	probably more widespread but doubtfully ever abundant.
Leptophytum laeve	1	very steep firm rock.	ST, 16–20.	—	—	—	—	inadequate data.	occasional small purplish crusts; probably much more frequent than recorded.
Lithothamnion glaciale	9	bedrock; boulders and stones stabilized on detritus.	ST, 0–12 (–30).	1	*Laminaria hyperborea* *Modiolus modiolus* *Cyprina islandica*	stipes shells shells	ST, 10–12.	probably continuous over local depth range.	often present as loose to embedded 'hedgehogs'; in field data, occasionally embraced within term Lithothamnia and therefore under-recorded; often main constituent of fjordic subtidal maerl; as underflora to *L. hyperborea* and in open at greater depths, usually admixed with *Cruoria* and *Pseudolithoderma*.
'Lithothamnia' (various forms)	5	steep/very steep/vertical/ overhung firm rock.	splash zone in small caves; IT mid to lower pools and wet; ST, 1–10+ m.	—	—	—	—	locally as continuous mosaic over site depth range.	probably several spp., forming more or less continuous base cover in absence of *Corallina*; all types, e.g. 'bracket-fungus' and crustose, included here as single entry; distribution certainly wider than stated.
Litosiphon filiformis	—	—	—	1	*Laminaria hyperborea* *L. saccharina*	laminae laminae	shallow ST.	sporadic.	recorded only in Skálafjørður.

Table 4 cont.

Litosiphon laminariae	—	—	—	3	*Alaria esculenta*	laminae	ST, fringe and shallows, 0–2 m.	locally common, but mostly discontinuous.	—
Lomentaria articulata	5	firm rocks or boulders.	see overall range column.	2	*Laminaria digitata*	holdfasts and bases	see overall depth range column.	shaded wet and pools, lower IT/ST fringe, shallow ST; locally continuous.	often abundant and/or luxuriant locally, but not frequent; usually as shaded underflora or epiphyte.
Lomentaria clavellosa	15	often steep surfaces of bedrock/ boulders; concrete-faced harbour walls.	lower IT in wet; ST, 0–20 m.	6 (3 epip. 3 epiz.)	*Laminaria hyperborea* *Furcellaria lumbricalis* *Ceramium shuttleworthianum* sponges (e.g. *Halichondria*)	stipes secondarily reattached to distal association (in/on/ through)	mid IT down to 15 m ST.	locally mosaic or stepwise distribution as epiphyte, often derived from substrate dis-continuities; locally more or less continuous epilithically.	epiphytes often small plants and never noted fruiting during study; often large plants epilithically or sponge-associated; frequently fruiting when epilithic— ♀ at 6 sites; ⊕ at 4 sites.
Lomentaria orcadensis	7	rocks/boulders, usually very steep to vertical; concrete-faced harbour walls.	see overall range column.	6 (all epiz.)	sponges (e.g. *Clathrina coriacea*; *Halichondria*) *Modiolus modiolus*	association (in/on/ through) shells	see overall range column.	locally restricted, but continuous overall; lower IT in wet, ST 0–12(–15) m.	apparently relatively intolerant of scour; prolific locally on vertical slopes with sponges; sometimes as *L. hyperborea*-underflora.
Membranoptera alata	12	firm rock; large boulders; stones stabilized in sand; concrete-faced harbour walls.	see overall range column.	13	*Laminaria hyperborea* *L. digitata* *L. faeroensis* *Furcellaria lumbricalis* *Patella vulgata*	stipes stipes stipes below tips shells	see overall range column.	locally continuous according to physical conditions; lower IT pools in shade; ST fringe and (0–)1–20 (–29) m.	specimens in exposure or below laminarians in depth are smaller; sometimes codominant *L. hyperborea* epiphyte in *c.*15–20 m; epiphyte or underflora to *L. digitata* in shallow ST.
Monostroma fuscum	1	firm rocks and large boulders.	wet low IT/ shallow ST.	—	—	—	—	data inadequate.	identified by E. M. Burrows.

Monostroma grevillei	—	—	—	10	*Corallina officinalis* *Dumontia contorta*	distal —	pools and wet places, MTL to ST. fringe	continuous locally over the restricted vertical range; details, see epiphytic range column.	very rarely on *Dumontia*; young whole sacs not infrequent.
Myrionema strangulans	—	—	—	2	*Ulva lactuca* *Monostroma fuscum*	— —	MTL, lagoons; lower IT, pools.	data inadequate.	recorded from sheltered conditions in fjords.
Myrionema sp.	—	—	—	3	*Porphyra umbilicalis* *Palmaria palmata*	— —	IT host as top shore band and in standing water; ST on *Palmaria* (on *L. hyperborea*) in shallow depths.	data inadequate.	perhaps more than one taxon, since 'hosts' differ.
Myriotrichia clavaeformis	—	—	—	1	*Scytosiphon lomentaria*	generally distributed over surface	lower IT.	as host, most probably.	probably much more widespread.
Odonthalia dentata	21	firm rocks or boulders, of variable slope.	ST, in 1–*c.*15 m.	3	*Laminaria hyperborea*	stipes	MTL pools in shade, to ST in 0–15(–29) m.	continuous as epilithic growths; mostly in upper levels (0–15 m) as epiphyte.	frequent as underflora; fine material in places (20).
Palmaria palmata	17	variously sloping firm rock; boulders in/on detritus; sloping concrete of slipways; concrete wall facings.	IT pools and wet places; shallow and deeper ST, 0–7 m.	15	*Laminaria* hyperborea (predominantly) *L. digitata* *L. faeroensis* fucoids	stipes (less often blades and holdfasts) stipes; holdfasts stipes stipes; holdfasts	as epilithic, but ST 0–12 m.	continuous over ranges; details, see range columns.	swards on lower IT mostly of 'sarniensis' form, some being ⊕; IT populations mostly epilithic; lower IT populations often massed and encouraged by freshwater down-flow (36; 37); ST populations below 2 m depths mostly epiphytic but shallows to 5 m show some epilithic underflora; ST epiphytes mostly of 'normal' morphology.

Table 4 cont.

Petalonia fascia	2	firm rock or large horizontal flat boulders.	wet MTL to shallow LWS channels.	3	*Chaetomorpha melagonium* *Corallina officinalis* *Gigartina stellata* various other algae and animals	surface distal distal —	lower IT to shallow ST.	mosaically continuous, where present.	occasionally as dense and continuous horizontal bands on IT rock.
Peyssonnelia dubyi	1	basal stones on bedrock.	ST, in 5–7 m.	—	—	—	—	inadequate data.	few patches detected; clearly rare.
Phycodrys rubens	24	firm rock and boulders; sometimes with sponges on verticals; boulders on detritus; concrete facings of harbour walls.	lower IT; ST, (0–)1–20(–30).	24	*Laminaria hyperborea* (predominantly) *L. digitata* *Gibbula*	stipes; less on holdfasts stipes	lower IT (*Gibbula*); ST fringe, +1 m (on *L. digitata*) to 24+ m (mostly 1–20 m).	continuous over depth range; see range entries.	epiphytic and epilithic to laminarian limits; epilithic only below; young on *Gibbula*; large normal plants in 0–15+ m, often fewer but individually larger with depth increase (site 19); deep water long-processed form below laminarians.
Phyllophora crispa	7	steep firm rock, often in shade; boulders and stones in detritus, especially in gullies; sometimes sponge-associated on verticals.	ST, (1–)2–16 (–22+) m.	2	*Laminaria hyperborea* *L. digitata* sponges (e.g. *Halichondria*)	holdfasts stipes in/through	ST, 0–2 m.	continuous, except for deep record at 22+ m outside cleft (site 31).	a single axis amongst collections possibly young *Phyllophora pseudoceranoides*; epiphytic only as young plants; epilithic as underflora to outgrading *L. hyperborea*, otherwise in gullies beneath latter.
Phyllophora traillii	1	under overhangs in very steep to vertical wall; part sponge-associated.	ST, 7–10.	—	—	—	—	data inadequate.	very rare; not dense at recorded location; not associated with *L. hyperborea*; epizoic status when sponge-associated doubtful.

Phyllophora truncata	6	boulders or stones in detritus, often in gullies.	ST, (0–)4–12(−20).	—	—	—	—	locally more or less continuous over range, except outlier record at 20 m.	under *Laminaria hyperborea* in gullies or sand patches; often largely sand-buried; large ♀ (4, 5, 24); deeper records involve larger plants but in smaller numbers.
Phymatolithon lenormandii	4	standing water or wet places on firm rock or stabilized stones and boulders; especially on vertical artificial surfaces in lower IT.	IT, lower levels; ST, shallows.	2	*Laminaria hyperborea*	stipes (patchily)	ST, *c.*5–7 m.	probably locally continuous, even ubiquitous at usual levels.	probably widespread and dense on firm substrates; distribution interrupted by detritus; under-recorded, since submerged in field-notes in places as 'Lithothamnia'.
Phymatolithon polymorphum	1	stones, boulders and containing bedrock, shallow sandy gullies.	ST, 4–8 m.	—	—	—	—	data inadequate.	probably much more widespread as underflora where canopy more spaced out.
Pilayella littoralis	2	firm rock; large boulders.	see overall range column.	6	*Laminaria digitata* other laminarians *Cladophora sericea* *Laminaria faeroensis* *Fucus spiralis* *F. vesiculosus* *Callithamnion sepositum*	laminae tips distal laminae laminae laminae distal and median.	see overall range column.	IT: mid to lower, pools and wet places. ST: shallow fringe in harbours; shallow ST proper to 2–3 m on open coasts. data inadequate for assessment of continuity.	sometimes only mixed with *C. sepositum* (site 23); unilocular sporangia at 15 amd (abundantly) 23; both plurilocular sporangia and longitudinally-dividing unilocular sporangia at 16B.

Table 4 cont.

Plocamium cartilagineum	21	firm, often steep, rock; boulders on bedrock or detritus; stones over/in detritus.	lower IT, in shaded pools; IT fringe; ST, 0–20 (–30) m.	9	*Laminaria hyperborea* *L. digitata* *Modiolus modiolus*	stipes holdfasts shells	IT, in lower pools; ST, (1–) 5–15(–22+)	usually continuous; locally step-wise (as at site 34), with gap between plants of *L. digitata* underflora (at *c.* +0·5 to 0·5 m) and *L. hyperborea* underflora (3–16 m)	epiphytic and epilithic flora to *L. hyperborea* or (less often) *L. digitata*; deeper records (20–30 m) all epilithic; occasional fringe records under *Alaria* (e.g. sites 29, 30); epiphytic plants mostly fewer but larger with increasing depths (site 19); some large epilithic plants in first 10 m depths (to 30 cm long); ♀ plants epiphytic (5–9 m) and epilithic (1–12 m); ⊕ plants small in shaded IT poolts.
Plumaria elegans	1	firm rock; boulders.	IT, mid to lower levels, in shaded clefts or verticals.	—	—	—	—	data inadequate.	shade plant very rarely detected; locally well-developed as pendant clumps on exposed parts of headland at *Callithamnion sepositum* levels.
Polyides rotundus	3	rocks/stones/ boulders in detritus.	IT, lower shaded pools; ST, 2–12 m.	—	—	—	—	patchily discontinuous with substrate, horizontally or vertically.	probably the least important of the detritus-tolerant species on the Faroes; see Table 5 for additional detail; subtidal plants usually under *L. hyperborea*; locally large clumps in good condition.

Polysiphonia brodiaei	2	moderately steep firm rock, often Lithothamnia-covered in wavewash.	see overall column.	2	*Corallina officinalis*	distal	see overall column.	widespread, but data sparse; lower IT and ST fringe: pools, shallow standing water, wet areas of *Corallina*.	epilithic status of specimens on Lithothamnia-covered rock not firmly established, probably only due to spread from vigorous epiphytic populations; other epilithic plants closely associated with *Corallina*.
Polysiphonia elongata	2	broken boulders of harbour wall; stones/boulders over gravel-on-mud or sand.	ST, shallows in range 1–9 m.	—	—	—	—	data inadequate.	single straggly clump probably wedged in mud (Skalabotnur); single individual plant at site 27.
Polysiphonia fibrata	—	—	—	6	*Corallina officinalis*	distal	lower IT pools, lagoons, or drainage channels.	locally abundant over range, but irregular and often lacking.	present locally in wave-action or in shelter; ⊕ (site 31); quantity present varies from masses (31) to rather little (37).
Polysiphonia lanosa	—	—	—	5	*Ascophyllum nodosum*	distal	IT, mid to lower; host fringe growths alongside *Alaria*.	locally continuous.	⊕ and ♀ at site 5; abundant to very dense growths on host, with *Dermocarpa* also present at 5; no growths seen on *Fucus vesiculosus*.
Polysiphonia nigrescens	3	IT, steepish to shallowly sloping rock, with shallow declivities; ST, stable stones and boulders in lagoon.	lower IT, pools and wet places; shallow ST.	—	—	—	—	patchy and not frequent.	infrequent ♂ (site 23); open rock flora, not underflora to canopy organisms.

Table 4 cont.

Polysiphonia urceolata	24	firm rocks and boulders, vertical to horizontal; stones in gravel/sand; concrete wall facings.	upper IT to 25 m ST, mostly in range low IT to 20 m; IT pools and wet places.	13	*Laminaria hyperborea* (mostly) *Corallina officinalis* *Himanthalia elongata* *Modiolus modiolus*	stipes (less often holdfasts) distal buttons shells in sand.	IT, standing water, to ST, 1–16 (–20) m.	locally and overall continuous.	more in ST than in IT; more often under *L. hyperborea* than epiphytic on it; forms 'fuzz' or tufts as epilithic underflora, often silt-binding in *Alaria* levels; patchily well-developed around 20–25 m depths; usually smaller as plants and as tufts in IT than in ST; epiphytes show sometimes massive growth (as at site 14).
Porphyra leucosticta	4	rocks and boulders; stabilized stones.	lower IT and shallow ST.	2	*Gigartina stellata* *Fucus distichus* ssp. *edentatus*	distal stipes	lower IT, pools and wet places.	locally scattered; data inadequate.	in exposure and shelter, not common, but possibly more widespread; tends to occur in open fjords and sounds.
Porphyra miniata	5	steep bedrock and boulders; larger boulders in stabilized sand.	ST, 0–9.	8	*Laminaria hyperborea* fucoids (*spiralis; vesiculosus; distichus* ssp. *edentatus; spiralis* f. *nana*) *Gigartina stellata*	laminae (often tips) laminae all distal	IT, mid to lower, in shaded pool depths or wet places; ST, 1–9 (–10+) m.	locally continuous.	usually associated with canopy laminarians in ST; some plants large in IT (as epiphyte, to 35 cm) and ST (at site 27, in 3–4 m, to 60 cm); releasing spores as epiphyte on *Gigartina*, at 19; heavy release from tattered plants in 6–7 m at 38.

Porphyra umbilicalis	15	upper shore firm rocks and artificial surfaces; boulders in sand; concrete facing of IT harbour wall.	see overall range.	1	fucoids barnacles	laminae (tips)	see overall range.	upper shore IT band, below *Verrucaria*, at 0·5 to 3 m above low water level; sometimes locally discontinuous.	widespread epilithic (mainly) and epiphytic (rather less) band sometimes to 1 m wide; variation in band vigour and width due to effects of freshwater downwash or drip, to configuration, and to pattern of wash upcarry; some overlap with *Prasiola* and *Blidingia*, occasional admixture with *Fucus spiralis*.
Porphyropsis coccinea	—	—	—	2	*Desmarestia aculeata*	distal parts	shallow ST to 10 m.	very locally abundant, both horizontally and vertically; overall sporadic to rare.	well-developed plants densely present at 36.
Prasiola stipitata	8	steep to moderately sloping firm rock; large boulders; bouldered artificial seawalls and moles.	IT, top shore, above and mixed with *Blidingia*.	—	—	—	—	top shore band varies locally from dense to patchy due to substrate and configuration.	often in areas affected by seabird droppings.
Pseudolithoderma extensum	14	firm rock; stones and boulders stabilized on bedrock or in detritus; concrete facing of bouldered harbour walls.	ST, 1–40+ m (1–4 m only on harbour wall and in Skálafjørður).	1	*Laminaria hyperborea* *Modiolus modiolus* *Cyprina islandica*	stipes shells shells	ST, 10–12 m (site 36).	continuous over local range, but depths vary a good deal from location to location.	underflora to *L. hyperborea* and penetrating depths below latter limits; usually admixed with *Cruoria* and *Lithothamnion glaciale*; needs space in canopy; locally few crusts in considerable depth; cover increases with depth over range.

Table 4 cont.

Pterosiphonia parasitica	7	firm rock, often steep or associated with steep surfaces; boulders.	IT, deep/shaded pools, MTL or LWL levels; ST, 5–13 m	—	—	—	—	stepwise (not present in shallow ST), but sample small for assessment.	often as *L. hyperborea* underflora or in clearings; mostly collected from 10–13 m depths.
Ptilota serrata *Ptilota plumosa*	15	bedrock; boulders; stones in sand gullies or otherwise stabilized; concrete-faced harbour walls; sometimes sponge-associated on latter.	lower IT, in shaded standing water; ST, in (0–)5–30 m.	16	*Laminaria hyperborea* *Gibbula* sponges	stipes (less often holdfasts) shells surfaces or in/through.	low wet IT on *Gibbula*; otherwise (0–)1–15 (–22+) m, in ST.	locally continuous, according to conditions.	considered together since normally so occur and no differences in ecology detected; plants on *Gibbula* in low wet IT only young; occurs as underflora and epiphyte to *Laminaria hyperborea*; deeper records (22–30 m) all epilithic; deeper epilithic plants only as rosettes on horizontal surfaces (sites 35; 44); epilithic/epiphytic balance variable with area.
Punctaria latifolia	—	—	—	1	*Fucus vesiculosus* *Laminaria faeroensis* *Laminaria saccharina*	laminae stipes; laminae stipes; laminae.	lower IT in wet; ST fringe.	data inadequate.	in very sheltered harbour conditions; plurilocular sporangia present in intertidal plants.
Ralfsia verrucosa	2	firm rock; shaded clefts between boulders.	see overall range column.	—	—	—	—	high to low IT; niche pools of vertical blocks upshore, wet places, lower shore; probably locally continuous but sample small.	in semi-exposed positions on headlands.

Rhizoclonium riparium	1	steepish firm rock.	see overall range.	2	*Laminaria faeroensis*	holdfast scrapings; laminae; stipes	see overall range.	upper mid IT; shallow ST in open fjords or sheltered shallow harbours to 2 m depths.	probably infrequent but more widespread than records suggest; with *Enteromorpha torta, Erythrotrichia carnea, Polysiphonia urceolata,* in holdfast scrapings; mixed with *Pilayella* in harbour; amongst *Bangia* in upper to mid IT; latter may include plants actually *on Bangia*.
Rhodomela confervoides	2	firm rock.	IT, wet lower levels; ST, 0–5 m.	1	*Laminaria hyperborea*	stipes	ST, 0–5 m.	locally continuous where present IT/ST.	locally abundant as epilithic growths, but apparently not common; see also entry for *Harveyella mirabilis*.
Rhodomela lycopodioides	2	firm rock and stabilized boulders.	ST, ELWS to 5 m.	—	—	—	—	inadequate data.	locally but rarely abundant, usually in shelter; more records in Skálafjørður.
Rhodophyllis dichotoma	See *Fimbrifolium dichotomum*								
Rhodophysema elegans	2	firm rock.	ST, above 10 m to 24 m.	—	—	—	—	inadequate data.	recorded with some reservations; plants from site 21 very possibly represent ?*Peyssonnelia*; records from Kumlavik (near site 23) are of plants with neither secretory cells nor reproductive organs.
Scytosiphon lomentaria	7	firm rock; boulders.	see overall range column.	2	*Patella vulgata*	shells	see overall range column.	locally patchy but not uncommon; upper and lower IT, pools, wet places, and washed positions; shallow ST, to 1 m depth.	records from shallow ST involve sheltered locations; *Patella* epizoic growth locations (sites 20; 37) were in wave-wash and upper pools.

Table 4 cont.

Sphacelaria cirrosa	—	—	—	1	*Cladophora rupestris*	distal	mid-tidal pools (IT).	inadequate data.	probably more widespread than recorded.
Sphacelaria plumosa	1	cobbles over rock and detritus.	ST, 4–6 m.	—	—	—	—	inadequate data.	probably more widespread than recorded.
Spongomorpha aeruginosa	—	—	—	3	*Chordaria flagelliformis* *Cystoclonium purpureum* *Laminaria faeroensis* *Cladophora rupestris*	distal distal holdfasts distal	standing water at IT fringe; shallow ST.	continuous, where present.	inconspicuous epiphytes on various other algae not specifically recorded in field data.
Spongomorpha arcta	12	firm rock; large boulders; concrete facings to walls and moles.	see overall range.	1	*Laminaria hyperborea*	lower stipes	see overall range.	upper IT to ST fringe, often (but not always) in wet places; shallow ST, to 1·5 m depth; locally continuous.	band-forming in IT; more often in semi-exposure than in shelter.
Spongonema tomentosum	—	—	—	1	*Ascophyllum nodosum*	distal	IT: lower mid-level, in shelter just within fjord.	inadequate data.	probably more widespread and frequent, as epiphyte.
Stictyosiphon griffithsianus	—	—	—	1	*Palmaria palmata*	general over frond	shallow ST.	inadequate data.	doubtful if ever frequent, but possibly more widespread.
streblonemoid browns	—	—	—	2	*Porphyra umbilicalis* *Devaleraea ramentacea*	general general	see overall range.	IT, host as top shore band in standing water; ST in shallows in 15 cm to 1 m depth.	neither biological nor taxonomic significance well known for these taxa; plants detected had filaments and pseudohairs.
'Trailliella intricata'		polythene bristles.	ST, *c*.8 m.	1	*Corallina officinalis*	distal, but not apical.	IT, tide pools and shallow flats low on shore, semi-	inadequate data.	*new records for Faroes;* very few gland cells in ST material from Skálafjørður.

Ulothrix flacca	1	concrete-faced boulder seawall.	see overall range.	1	*Antithamnion floccosum*	distal, with *Audouinella* sp.	see overall range.	ELWS and shallow ST fringe; locally band-forming, but markedly discontinuous.	locally very dense growths in some sheltered harbour conditions; fertile.
Ulothrix sp.	1	steep rocks and boulders.	mid to lower IT.	1	*Enteromorpha* sp.	median	mid to lower IT.	inadequate data.	may be one or two undetermined taxa involved; material from site 13 formed tufts intermeshed with basal flora; site 16B plants were epiphytic or enmeshed with 'host'.
Ulva lactuca	18	firm rock; boulders; stones stabilized in detritus; concrete-faced walls.	lower IT, pools and wet places; ST, 0–20 m.	8	*Corallina officinalis* *Laminaria hyperborea* *L. saccharina* *L. faeroensis* *Fucus vesiculosus* *Modiolus modiolus* barnacles	distal stipes stipes stipes laminae shells shells	low IT, pools and wet places; ST, 0–12 m.	some discontinuities between shallow growths and deeper populations; no ST epilithic records between 10 and 20 m, no ST epiphytic records between 5 and 10 m.	often amongst other algae, commonly *Enteromorpha linza* and *E. intestinalis*, as epilithic growths; subtidal plants often large in open, smaller when (as rarely) present within forest of *L. hyperborea*.
Ulva rigida	1	firm rocks and wetted boulders.	lower IT.	1	*Laminaria faeroensis*	holdfasts	shallow ST.	data inadequate.	infrequent, especially in IT, amongst *Ulva lactuca*; probably under-recorded.
Urospora ?mirabilis	1	rocks/boulders.	HWM.	—	—	—	—	clumps forming a (?) discontinuous band.	sparsely, probably much under-, recorded; good state of detected material would suggest the species is more widespread.

Table 4 cont.

Urospora penicilliformis	2	concrete-faced bouldered seawall; separate boulders.	lower IT.	1	*Fucus distichus* ssp. *anceps*	laminae	lower IT.	data inadequate.	epiphyte and underflora to fucoids on semi-exposed heads.
Urospora wormskjoldii	—	—	—	1	*Fucus distichus* ssp. *anceps*	laminae	lower IT.	data inadequate.	tufts on fucoid, semi-exposed head; under-recorded ?
Urospora spp.	1	shallowly sloping washed rocks.	upper IT.	—	—	—	—	data inadequate.	not easy to align with other *Urospora* taxa, but only local growths available; possibly all material conspecific with the *U. ? mirabilis*.
Waerniella lucifuga	2	large cave-like crevices between boulders; deep shaded and large swell caves, roof and walls.	IT, usually high on shore (to 5 m above LW) in swell-cave sites.	—	—	—	—	probably almost continuous in appropriate-conditions.	wet shaded conditions appear obligate; probably much more widespread in the many examples around the Faroes.

TABULAR NOTES

1. Species of canopy flora and other taxa dealt with in more specialized contexts in other tables are generally excluded.
2. *Notes* column includes available data on fruiting; distribution; status; vigour; ecology; general points.
3. *Overall depth range characteristics* column covers both amplitude and distribution characteristics within amplitude, as required.
4. Abbreviations employed throughout include IT = intertidal; ST = subtidal; ELWS = extreme low water of spring tides; LWS = low water of springs; MTL = mean tide level; LWL = low water level; HVM = high water mark; LW = low water.
5. Bracketed light-face numbers in notes and elsewhere are station/site numbers; where used, bold-face **(1)** refers to epilithic characteristics, bold-face **(2)** to epiphytic/epizoic characteristics.
6. Depths are *below* ELWS unless + sign appears.
7. ⊕ = tetrasporangia; ♂ = spermatangia; ♀ = carpogonial branches; **♀** = carposporophytes.
8. Endophytic or 'parasitic' records are included as epiphytic records, with comments; endozoic records are similarly treated as epizoic.

very steep rock surfaces overgrown by sponges, or detritally-scoured or detritus-covered situations do, of course, carry somewhat specialized flora; even then, there is a large measure of overlap represented by the more widely tolerant species.

Laminaria hyperborea epiphytes and underflora

It will be clear from Table 4 that there are relatively few *L. hyperborea*-associated subordinate species that have not been recorded as both epiphytic and epilithic at, as a minimum, a few of the stations on the Faroes. Many of the more consistent, abundant and luxuriantly-developed constituents of the subordinate flora in *L. hyperborea* levels are more or less equally often noted epiphytic as they are epilithic. The species *Ceramium rubrum* (not restricted as to level or host, as an epiphyte) is a case in point (11 station records as epiphyte; 11 as epilithic growth). Others are *Palmaria palmata* (15, 17), *Phycodrys rubens* (24, 24), *Polysiphonia urceolata* (13, 24), *Callophyllis cristata* (15, 20), *Membranoptera alata* (13, 12), *Ptilota serrata/Ptilota plumosa* (16, 15), and *Ectocarpus fasciculatus* (4, 4).

Many species amongst the more frequently-recorded subordinate taxa demonstrate more bias of occurrence in one state than in the other. Principally recognized in epiphytic situations, very often on *Laminaria hyperborea*, are *Fimbrifolium dichotomum* (4, 2), *Porphyra miniata* (8, 5), and *Pilayella littoralis* (6, 2). More species are recorded principally in epilithic subordinate situations and less frequently as epiphytes. These include *Audouinella purpurea* (6, 2), *Lomentaria clavellosa* (15, 3), *Spongomorpha arcta* (12, 1), *Corallina officinalis* (17, 1), *Ulva lactuca* (18, 8), *Callophyllis laciniata* (21, 10), *Desmarestia viridis* (19, 1), *Pseudolithoderma extensum* (14, 1), *Cruoria pellita* (14, 2), *Phyllophora crispa* (7, 2), *Phymatolithon lenormandii* (4, 2), *Lithothamnion glaciale* (9, 1), *Delesseria sanguinea* (18, 5), *Chaetomorpha melagonium* (10, 4), *Plocamium cartilagineum* (21, 9), *Antithamnion floccosum* (3, 2), and *Odonthalia dentata* (21, 3).

A few more or less widespread species, such as *Dilsea carnosa, Lomentaria orcadensis, Pterosiphonia parasitica, Desmarestia aculeata, Desmarestia ligulata, Phyllophora truncata, Gigartina stellata, Cladophora rupestris, Polyides rotundus,* and *Bryopsis plumosa,* all appeared to be confined to subtidal and low intertidal epilithic conditions along Faroese coasts.

Instances amongst these lists for which the balance in favour of epilithic or epiphytic preference seems slight have been allocated because of the abundance and luxuriance of growth in the one habitat state as opposed to the other. *Antithamnion floccosum,* for example, was tantamount to locally band-forming in its epilithic situation in the shallow subtidal at Tinganes (station 16B), and was present in substantial amounts in its other non-epiphytic locations. As an epiphyte on *Aglaozonia (= Cutleria),* itself on *Laminaria hyperborea,* by contrast, the species was recorded only as fragments or as very small numbers of individuals. Similar adjustment of allocation has been made in other cases where comparative abundance and/or luxuriance outweighed the actual numbers of station records, where these latter were not dissimilar, although in a great many cases the frequency and abundance of appearance tended to be similarly biased. It should be noted that we have here avoided basing major reasoning on any taxa for which there is even occasional difficulty in deciding what is or is not epiphytic/epilithic growth, although where attainment of 'adult' growth clearly results in/from epilithic growth-attachment in circumstances where we are not sure whether any early reproductive element stages were actually initially attached to basal fragments of other algae, we have counted the instance as epilithic. Other doubts have been subject to comment in the individual species entries in Table 4.

Epiphytes and underflora to other major subtidal organisms

Much of the necessary consideration of underflora species concerned has been presented in the section above on *Laminaria hyperborea* associates; subtidal depth tolerance of most of the significant underflora species includes the levels at which *Alaria, Laminaria digitata, L. faeroensis,* and *L. saccharina* have variously been detected. Density or luxuriance variations are more reactions to conditions derived from wave-shelter or wave-exposure in these (comparatively shallow) depths than they are to the actual depths involved. Major epilithic subordinate species, such as *Plocamium cartilagineum, Odonthalia dentata, Lomentaria clavellosa, Spongo-*

morpha arcta, Corallina officinalis, Desmarestia viridis, D. aculeata, Polysiphonia urceolata, Delesseria sanguinea, and *Ulva lactuca,* include both wet intertidal or subtidal fringe situations and the subtidal itself within their tolerance limits. This statement is also true for major subordinate taxa that appear equally to exploit epilithic or epiphytic situations, for example *Callophyllis cristata, Ceramium rubrum, Membranoptera alata, Palmaria palmata, Phycodrys rubens,* and *Ptilota serrata.*

Certain epiphytes are restricted to growth on the other major subtidal canopy organisms, although once again the more visually impactful and vigorous epiphytic species, as with the facultative taxa, are more tolerant and appear on all canopy species. *Lomentaria articulata,* mostly epilithic but occasionally noted epiphytic, appears on the holdfasts and stipe bases of *Laminaria digitata,* usually by spreading from adjacent epilithic growths. *Audouinella alariae* and *Litosiphon laminariae* are confined to the laminae of *Alaria esculenta*; although not widespread, both species are locally vigorous and occasionally *Alaria* plants stand out because of extensive epiphyte growth over the whole lamina, particularly where *A. alariae* is involved. *Spongomorpha aeruginosa* occurs on a number of hosts, including the holdfasts of *L. faeroensis* within fjords. Various records of species within the genus *Giffordia* have been established from the stipes of *Laminaria digitata. Dictyosiphon foeniculaceus, Asperococcus fistulosus, Punctaria latifolia, Chordaria flagelliformis, Rhizoclonium riparium, Ectocarpus siliculosus,* and *Pilayella littoralis* all appeared wholly or mainly, when epiphytic, on laminarians other than *Laminaria hyperborea*, although most were also detected on larger plants of genera other than *Laminaria.* Fuller details appear in the summary presented as Table 4.

iii. Subtidal: other specialized situations

Detrital conditions

Large numbers of species occur in potential connection with some degree of detrital scour and movement along open shores, in that small boulders and stones resting *on* the detrital surface in calmer situations, and similar substrata stabilized *in* the detrital underlayer, will occasionally support the usual form of epilithic underflora, and even sometimes a canopy layer. It will be clear from consultation of the individual species entries in Table 4 which of the underflora constituents are tolerant to this degree. Canopy species also involved have been dealt with earlier in this paper. A small number of species is, with a high degree of consistency, customarily associated with growth more fully in, or more generally *through* (from the underlying rock or boulders to which the plant has attached), detrital substrata. On the open shores of the Faroes, the most commonly present species in these conditions are *Furcellaria lumbricalis, Polyides rotundus, Phyllophora truncata,* and *Ahnfeltia plicata*. Distribution characteristics of these species are summarized for Faroes locations in Table 5. Despite the relative frequency of *Ahnfeltia plicata* in the conditions described, we did not detect any of the occasional pure societies over fairly large areas reported by Børgesen (1902: 360). *Polyides* was noted by Børgesen (1902: 398) as growing on stony bottoms in deeper water and sheltered conditions, which implies but does not state involvement of detrital substrata. He also (1902: 397) indicated *Furcellaria* from stony situations in fair exposure. *Phyllophora truncata* (as *P. brodiaei*) was reported as dispersed and mostly in small quantities on, most commonly, sheltered stony bottoms. There is some general suggestion here of agreement with our findings.

A high percentage of the customary floras of inner portions of fjords and of the middle sections of sounds is also represented by species with considerable tolerance of instability (which is often associated with detrital conditions) in the substrate. Such species are listed in summarized detail throughout Table 4 and are dealt with more fully on population and community ecology bases by Tittley *et al.* (1982), as well as earlier by Børgesen (1905).

Epizoic growth and animal associations

Børgesen presented no detailed analysis of the erect species habitually or frequently growing on or with animals as substrata or as life-associates, although he did (1905: 760; 761) comment on (i) certain red, green and blue-green endophytes and boring forms customarily present in shells at depths greater than the laminarians, and (ii) red algae consistently present in bryozoans. Shells of various invertebrates are mentioned as substrata in the individual species entries in his 1902 paper. For varied reasons (blanket spore outfall at certain intertidal or subtidal levels; absence of other firm substrata in a particular micro- or macro-area; non-browsing of elements settled on animal structures), some algae appear wholly or strongly so associated over their distributional areas along shores of the Faroes. Other species are clearly able occasionally to tolerate the environment provided by the animal structures concerned, even when they rarely seem to occur on the structures in the general event. Save for the grounds of pure chance, it is often not possible to postulate one of the above or other reasons for such growth. A summary of the species noted in our studies appears within Table 4 listings; in most cases the entries are self-explanatory but a few of the more unusual or consistent associations warrant detailed comment here.

The presence of broad swathes of particular invertebrates as bands or as dense local areas of coverage in particular intertidal and subtidal levels or patches makes the successful settlement on them of certain algae characteristic of those same levels/conditions almost inevitable. Such, for example, is the case intertidally with *Callithamnion sepositum* and subtidally with many species that occupy comparatively wave-exposure-free areas of sounds and fjords, and to a lesser extent protected coves on open coastlines. *Callithamnion sepositum* tends to occur as a broad band variously situated, according to configuration of the shore area and the extent of exposure to water movement, between the lower littoral fringe as lower limit and upper mid-tidal level where water is upcarried by cut channels in steep faces. With the blanket settlement that this represents in the presence of dense growth and high reproductive vigour, growth to maturity on *Patella*, barnacles, small *Mytilus* and all otherwise free rock/boulder surfaces, as well as on those algae (such as *Corallina, Gigartina stellata, Himanthalia,* and *Porphyra umbilicalis*) capable of withstanding the strain, is not surprising. Species characteristic of sheltered coves, fjordic areas, and sound areas are often confronted by the need to attach where the only available substrata set in otherwise mobile detritus are stones/small boulders and various bivalves, principally *Modiolus modiolus* and *Cyprina islandica*. Settlement recorded on one or both those animal shells is therefore to be expected and includes *Lithothamnion glaciale, Chaetomorpha melagonium, Lomentaria orcadensis, Ulva lactuca, Cruoria pellita, Plocamium cartilagineum, Pseudolithoderma extensum, Phycodrys rubens, Polysiphonia urceolata, Desmarestia aculeata, Laminaria saccharina,* and *Laminaria faeroensis*.

A fairly consistent set of associations that Børgesen seems not to have detected sufficiently often for comment, perhaps because they are rarely directly to be seen in shallow depth from the surface and are not readily observed in drift or dredged material, concerns various algae and various sponges. Certain algal species occurred almost habitually in sponge associations, growing on, with, or through the sponges concerned (mostly *Clathrina coriacea, Halichondria,* dead man's fingers, and certain unidentified white sponges). Consistent associations, often on steep to vertical rock or concrete-faced walls, were detected with *Derbesia marina, Lomentaria orcadensis*, and *Halicystis ovalis*, and less frequently or consistently with *Lomentaria clavellosa* (0–7 m, on harbour walls), *Callophyllis cristata* (1–9 m, on harbour walls and adjacent rocks), *Ptilota serrata* (1–9 m), *Callophyllis lacinata* (5–7 m, small plants with *Halichondria*), *Phyllophora crispa* (5–10 m, small plants on vertical faces), and *P. traillii* (7–10 m, on overhanging walls). The extent and form of the association was variable in the case of *Derbesia marina*. Direct growth on the sponge surface amongst *Laminaria hyperborea* on steep rock or artificial concrete (harbour) wall surfaces was quite often noted in depths of 0–7 m at different stations. In the outer parts of the main cleft at Gjógv (station 31), again on a very steep rock wall, most of the detected *Derbesia* grew (with the *Halicystis ovalis* stage) on *Corallina officinalis*, the latter itself associated with sponges over the range 2–10 m depths. In greater depths (about 18–20 m depths), although not a frequent occurrence, occasional good clumps of *Derbesia* grew fringing dead man's finger sponges at station 35. In depths beyond the 7 m that covered most of the vertical or very steep walls that we examined, *Derbesia* was mostly sparse to rare at even those few stations for which plants were detected (e.g. at 25 and 29). Despite the consistency of the *Derbesia*–sponge association at stations studied by us, it seems not always to apply. Børgesen

Table 5 Detrital flora—the characteristic species and their distribution.

Species	Station	Detrital substrate	Configuration	Depths (m)	Notes
Furcellaria lumbricalis	5	sand	on rocks/stones under sandy patches	7–12	Not fruiting.
	7	sand	in uneven channels between large boulders.	8–17	Large amounts of big plants; sterile.
	18	sand/silt	in few shaded detrital pools	lower intertidal	Not fruiting.
	19	sand	on small stones/boulders in frequent patches	5–9	Not fruiting.
	24	sand	stones or buried bedrock in sand-covered gullies in forest	4–8	Extensive clumps of non-fruiting plants.
	28	sand	on/in shallow sandy patches on bedrock amongst forest	5–7	Not fruiting.
	32	sandy silt	shaded undercut, in protected side of lower shore pool	low water of spring tides	Not fruiting; good clumps with encrusting epiphytic corallines; west side of cove behind Litlanes.
	32	mixed sand/gravel/silt	small stones in detrital shallows	3–4	meadows in shallows along east side of cove; not fruiting.
	33	sand	in gullies under forest	2–3	Not fruiting; half buried in sand.
	34	sand	in runnels and gullies	7–16	Not fruiting; with epiphytic *Ceramium rubrum*

Polyides rotundus	23	sandy silt	on rock surface buried in substrate, shaded shallow pool	lower intertidal	Large local clumps; not fruiting.
	33	sand	in gullies under forest	2–3	Half buried in sand; not fruiting.
	35	sand/gravel	on stones/rocks in substrate	10–12	Clumps in good condition; not fruiting.
Phyllophora truncata	4	sand	on small stones buried to 8 cm in gullies	*c.* 10	Cystocarpic.
	5	sand	on stones in sandy patches	7–12	Cystocarpic.
	24	sand	on boulders/stones in sand-covered gullies in forest	4–8	Cystocarpic.
	33	sand	on boulders/stones in sand	2–3	Not fruiting.
Ahnfeltia plicata	5	sand	on stones in sandy patches	7–12	Not fruiting.
	13	sand	on stones/bedrock in sandy pools	lower intertidal	Not fruiting.
	19	sand	on small stones/boulders in patches under forest	5–9	Not fruiting.
	20	sand	shaded deeper parts of a few pools	lower intertidal	Good bushy and wiry plants; not fruiting.
	24	sand	stones in gullies within forest	4–6(–9)	Not fruiting.

(1902) mentioned for that year a fairly abundant find of the species at about eight fathoms (*c.*15 m) on a rather exposed stretch at Hvidenaes, where it grew on *Balanus* and *Serpula*; sponges were not apparently present, or at least not mentioned. *Lomentaria orcadensis* sometimes, in the median depths of its range (0–12, less often to 15 m) as sponge associate, produced some beautiful material (as at station 14). Most of the records were established in the first 10 m of the subtidal, although a few plants grew on and through orange sponges in 10–12(–15) m on the very steep rock-face at station 29. We have recorded (see Table 4, the species entry) instances of *Lomentaria orcadensis* growing on substrata other than sponges and without sponge-association; however, our records do not include epiphytic material from *Laminaria hyperborea,* as mentioned by Børgesen (1902: 366), nor do any reach the 10–15 fathoms that he indicated for those Koltur epiphytes. The fair degree of frequency with which we recorded this species indicates that Børgesen's statement about 'rather rare' now represents a more apparent than real phenomenon for the Faroes.

A number of these sponge associates also occurred in conjunction with other invertebrates in the subtidal. *Callophyllis cristata,* for example, by no means confined to epizoic growth in any case, was recorded also from barnacles under *Alaria* (station 29) in 0–8 m; although cystocarpic, the plants were small, averaging 2–3 cm in length. Similar small, much-dissected plants occurred in shallow depths (0–1 m) on *Gibbula* in Hvannasund. *Ptilota serrata*, from that same location and depth, also grew on *Gibbula,* but young plants only were noted. Plants not detected as sponge-associated species but growing on other subtidal animals included *Callithamnion decompositum* (on serpulid worm tubes), recorded at 10–15 m; *Phycodrys rubens,* observed on *Modiolus* (see above) in 16–18 m in Sundini, noted as young plants with *Ptilota serrata* and *Callophyllis cristata* on *Gibbula* in 0–1 m (Hvannasund); *Rhodomela confervoides,* recorded at just below ELWS in Skálafjørður on *Mytilus; Membranoptera alata*, similarly present in the subtidal fringe, as in lower shore shaded niches, on *Patella*. This latter overlap tendency with the intertidal was emphasized by *Ectocarpus fasciculatus,* growing on many invertebrates as clumps in lower littoral and subtidal to 1 m depth in the lagoon adjacent to the Hvannasund Causeway.

Ectocarpus fasciculatus occurred intertidally epizoic in upcarry grooves on *Patella* (station 19), shells of which (station 37) bore a few clumps of *Scytosiphon lomentaria* in upper shore pools on steep rock. Washed lower shore to mid-shore open rocks in semi-exposed positions (e.g. station 20) and lower shore pools in shelter from direct wave-action (station 42) also showed *Patella* with epizoic *Scytosiphon.* This last station revealed masses of *Petalonia fascia* attached on mid- to lower intertidal invertebrates. Upper shore bands, occasionally reaching down to near low water level, of blanket epilithic/epiphytic/epizoic *Porphyra umbilicalis* on invertebrates (including especially barnacles), were noted on the steep to undercut but low water's edge cliffs at station 19. This same situation revealed barnacles also carrying *Blidingia minima, Enteromorpha intestinalis* and *Ulva lactuca,* none especially high on the shore.

Amongst algae noted by Børgesen (1902) as growing in or on invertebrate shells and/or skeletal tissue at various depths, we did not so detect (sometimes possibly because they were not specifically sought) *Pterosiphonia parasitica, Antithamnion plumula, Rhodochorton (Audouinella) membranaceum, R. (Audouinella) penicilliforme, Peyssonnelia dubyi, Phymatolithon laevigatum, Dermatolithon hapalidioides, Chorda filum, Gomontia polyrhiza,* and *Ostroebium quekettii.* Many of these listed species (e.g. *Pterosiphonia parasitica, Antithamnion plumula, Chorda filum, Audouinella penicilliforme*) have been recorded by us from other substrata.

Pools and standing waters

Algal species' tolerance of both intertidal and subtidal conditions, and the overlap in floristics that this produces, are both emphasized by the presence of 'permanent' standing waters and pools between the tidal limits, especially at mid-shore, lower shore, and subtidal fringe levels. Essentially, these waters and their immediate surrounds represent a selectively up-carried microcosm in conditions which repeat many of the phenomena of the transition at subtidal fringe levels from subtidal to true intertidal. This is to a degree true for coastlines in all parts of the world, but is emphasizedly so in such conditions of generally low insolation and relatively high humidity as apply along Faroese shorelines. Caves, not considered here since our observations were too restricted, similarly if to a lesser degree and for reasons of shading, swell-run and moisture-retention, affect the upward extension and 'intertidal' penetration of commonly subtidal and fringe forms. Our restricted data do not show marked disagreement with the section in Børgesen (1905: 739–742).

The extent to which intertidal standing waters encourage occurrence of selective up-carry and the principal species involved will be clear from a perusal of entries in Table 4. Relatively few, even intertidal, algae (some of which are mentioned in the next section; Børgesen, 1902: 736–737, also covers these) are not encouraged by the consistent presence of at least atmospheric moisture into denser, more luxuriant, more abundant and more reproductively effective growth than would otherwise have been possible. Subtidal species with a requirement for total or near total submergence do not appear above the shallow subtidal in the absence of standing water at these higher levels. A few subtidal species did not appear in the standing waters of Faroese open shore intertidals, presumably as a result of rarity (at range peripheries or for other reasons) creating an inadequate reservoir of reproductive elements. Examples include *Brongniartella byssoides* and *Derbesia marina.* For certain other species that did not appear in the intertidal waters (e.g. *Rhodomela lycopodioides, Fimbrifolium dichotomum, Callophyllis laciniata, Antithamnion plumula, Desmarestia viridis, Desmarestia aculeata, Pseudolithoderma extensum, Cruoria pellita,* the *Phyllophora* spp. (*P. traillii, P. truncata, P. crispa*), *Lithothamnion glaciale, Porphyropsis coccinea*) it is less easy to suggest explanations since they are essentially northern or widespread taxa that could be expected to tolerate the available physical conditions in adequate densities for maintenance of a large reproductive reservoir. In relatively nearby island groups (e.g. the Shetlands and Orkneys), as well as in northern Scotland, various of the species listed are at least locally common in shaded/deep intertidal standing waters. Some of these species have, indeed, previously been reported intertidally for the Faroes by Børgesen, so that our failure to record plants in the same circumstances may reflect local changes or seasonal variations; Børgesen's work was conducted over much of the seasonal variation pattern, in different years, whilst our period on the islands was more restricted. Cases in point, recorded intertidally by Børgesen, were *Rhodomela lycopodioides* and *Cruoria pellita* (the latter frequently in caves).

iv. Intertidal

As indicated in the introduction, descriptions of open shore species distributions presented by Børgesen were extremely good and largely are still valid. Although the major bias of our field-work was lower intertidal and subtidal, possibly leading to some under-recording of organisms (other than principal band-forming or condition-indicating species) more representative of higher shore levels, the middle and upper levels of the intertidal were by no means neglected and some differences in findings exist between ourselves and Børgesen (1902; 1905). We certainly recorded *Hildenbrandia* very high above low water, especially in caves (see Table 4); however, neither it nor *Ralfsia,* usually lower down shore as Børgesen (1905: 711–712) indicated, were so frequently recorded during our studies that they could be used to characterize either formations or associations (*sensu* Børgesen). As explained elsewhere, save for at station 19, we rarely profiled in detail the intertidal; at station 19, the levels which could have been expected to demonstrate strong *Ralfsia* and *Hildenbrandia*, from Børgesen's descriptions at least, bore only *Verrucaria*, referred to by him as one of the crustose lichens characterizing the uppermost parts of his exposed shore *Hildenbrandia* formation. For the immediately succeeding formation in the downward sequence that he reported, Børgesen (1905: 712 *et seq.*) utilized Chlorophyceae in characterization; the genera *Prasiola, Enteromorpha* and *Rhizoclonium* were mentioned. Locally dense bands of *Prasiola stipitata* were certainly consistent on appropriate steep to moderately sloping firm rock and boulders, or bouldered seawalls, in wave-washed situations. *Enteromorpha intestinalis* was also strongly present in standing water or wetter areas, often forming dense and wide swards. *Rhizoclonium riparium* we generally found lower on shore, well below or in the lower reaches of the *Blidingia minima* band that customarily overlaps from below with the *Prasiola* band. As indicated by Børgesen (1905: 742–743), the sheltered shore *Prasiola* levels may show a stronger presence of *Enteromorpha intestinalis* and rather less *Prasiola* than on more exposed upper intertidals. *Porphyra umbilicalis*, the characterizing organism of Børgesen's '*Porphyra-Association*', occasionally abuts directly below the *Verrucaria* levels (Børgesen's *Hildenbrandia* or Chlorophyceae-formations), as indicated in the entry in Table 4. Organisms that can be attributed to any of these levels are often locally mosaically intermixed on exposed rocky shores here, and it can frequently be difficult to decide which can be considered as primary characterizers, which as 'subvegetation' (*sensu* Børgesen). The latter author virtually acknowledged the existence of this complexity in his consideration of the *Porphyra*-Association (1905: 716–717). Nevertheless, we agree that levels below the *Prasiola-Blidingia* characterized areas are generally in wave-wash dominated by locally-dense clumped bands of *P. umbilicalis*. This applies equally on natural or artificially-faced surfaces at appropriate levels.

Reference to Fig. 4, head profile, will indicate some disagreement with other statements made by Børgesen (1905: 718). The clear barnacle upper limit there occurs mid-way between the upper and lower limits of the *Porphyra umbilicalis* band, this on a semi-exposed headland and in a locally greater degree of shelter from direct strong wave-beat. According to Børgesen, sheltered places bore lower limits of *P. umbilicalis* that were almost identical with the sharply-marked upper limits of *Balanus*; exposed shores showed *P. umbilicalis* not coming in until far above high water mark. In our sufficiently detailed studies, overlapping of the lower limit of *P. umbilicalis* to a considerable degree with the upper clear limit of barnacles was common on semi-exposed or sheltered steep to moderately-sloping rocky shores.

Bangia and *Urospora* were not noted as frequently, as densely, or as widespread by us as by Børgesen, although *Bangia* at least was usually at the sort of shore level that he described. Both organisms were also found lower down shore than indicated for his '*Bangia-Urospora-Association*'. It may be that our view here is coloured by the extent to which our detailed observations were logistically determined by appropriate diving sites, thus excluding some of the more exposed intertidals from greater than passing examination. However, detailed examination of sites with exposed populations of *Callithamnion* would seem likely to have offset any ill-balance derived from diving logistics.

In general, Børgesen's detailed observations agree with our own on (i) exposed and sheltered-shore Fucaceae; (ii) *Callithamnion sepositum* and its associates; (iii) *Palmaria palmata,* including its narrow-lobed ('*sarniensis*') form that occurs as swards, especially in freshwater downwash, along the open outer stretched of some fjords/sounds; (iv) the littoral *Corallina* populations (although its suggested frequent co-associate, *Lomentaria articulata,* was much less common amongst our records than indicated by Børgesen, 1905: 730); (v) *Monostroma grevillei*; (vi) *Spongomorpha arcta* (as *Acrosiphonia arcta* in Børgesen's treatment)—*Polysiphonia urceolata* (although we did not find, even 'very rarely', the *Cladostephus spongiosus* which he referred to as amongst the dense characterizing growths); (vii) *Gigartina stellata*; and (viii) *Himanthalia.* This will be clear from the profile details for station 19 and from the individual species entries in Table 4. It is, however, worth stressing that the points made elsewhere (in the earlier section on epizoic and other animal associations) regarding the wide range of substrata exploited in blanket populations, such as those usually present of *Callithamnion sepositum* on all but the most sheltered open Faroese shores, are insufficiently considered in Børgesen's text (1905: 725–727).

5. Discussion and conclusions

i. General

Northern areas, such as the Faroes, with comparatively uniform temperature conditions, frequent rain and fog, and comparatively consistent strong water movement on shores, show fewer profound effects of insolation and desiccation on the open-shore intertidal flora than do areas further south. Conditions are fairly similar, for example, to those in the Shetlands, Orkneys, and northern/eastern Scotland, but are markedly dissimilar to those in southern England. Background information on this is fully presented and explained in Børgesen (1905).

As a consequence, those species and groupings for which the Faroes represent part of the non-peripheral area of the distribution range usually appear in abundance, particularly where their ecological tolerances enable them to exploit the open intertidal and shallow subtidal shore levels. In its turn, this abundant representation often produces the 'blanket' effect in availability of reproductive elements, thus further emphasizing intensive colonization of even marginally tolerable environmental conditions. Organisms which are acceptable indicators, individually or in particular groupings, of exposure to strong water movement (commonly associated with wave-action) on English shores are therefore less reliably so on the Faroes; this comment would also be true for, as an example, *Callithamnion sepositum* in northern and eastern Scotland, where vigorous populations produce the blanket effect and penetrate more deeply into coves and inlets with lesser direct effects of wave-action than ever do the populations present along southern and western British shores. Biotic groupings that involve algal species such as *Alaria esculenta, Gigartina stellata, Ceramium shuttleworthianum, Callithamnion sepositum,* and (to a lesser degree) *Himanthalia elongata* are therefore less directly effective indicators of comparative exposure to water movement between open and fjordic shores on the Faroes. *Alaria* and *Ascophyllum nodosum* often occur side-by-side, both in vigorous stands, in the outer stretches of fjords and throughout the lower intertidals/subtidal fringes of sounds around the islands (e.g. at stations 23 and 35 (Ánir)). More sheltered areas of coves or inlets between semi-exposed headlands on open shores also often bear this juxtaposition, as at station 18 (Tórshavn–Hoyvík), whilst less frequently the phenomenon is met in wide and open bays between exposed headlands, as at Kirkjubøur (station 13). In Great Britain, *Alaria* is a dependable indicator of wave-exposure, whilst *Ascophyllum* is an excellent wave-shelter indicator.

The considerable size of many fjords and sounds, and the relatively small and localized freshwater run-off effects, both tend to emphasize resemblances between open and fjordic shores. Most of the organisms named throughout are present in similar positions and proportions deep into fjords, often to at least 2/3 of the length and (for some organisms) up to what is now functionally the fjordic head. An unusually clear example of this distribution type, created by artificial causeway construction in Hvannasund, has been fully considered in Tittley *et al.* (1982).

Of the potential indicator organisms named above, *Himanthalia* perhaps accords best here with the status allotted to it as an indicator of strong water-movement along British and adjacent shores. Even that requires circumspection in its use (at station 18, for example, the species occurred in coves and inlets alongside both *Ascophyllum* and *Alaria*), and the discussions which follow should be read in the light of such intertidal and subtidal differences from more familiar shores further south in the Atlantic.

An overall comparison of our observations against those of Børgesen and of more recent workers shows that, although we have not employed Børgesen's terms 'association' and 'formation', disagreements with broad outlines of his major ecological findings are few and mostly any differences are of local application or of detailed distribution. Such points are considered in the sections which follow. We have considerably elaborated information on the previously less clearly presented subtidal distribution patterns, whilst largely leaving aside the intertidal patterns, already more or less effectively dealt with by (especially) Børgesen, and more recently by others (Rex, 1970; Holt, 1975).

Except as regards the particular new records, or for rare or unusual species (discussed later), no phytogeographical treatment is presented here. Børgesen (1904) and Børgesen & Jónsson (1905) published particularly useful considerations of these aspects, and those considerations have very recently been updated by Irvine (1982).

ii. The subtidal

Børgesen (1905: 700–701) has suggested that the small amount of sun and light along the coasts of the Faroes may account for the fact that the marine algal vegetation does not grow at depths greater than 25–30 fathoms (*c.*45–55 m). He managed to obtain some well-developed Florideae at 25 fathoms, but nothing deeper than that; he indicated that disappearance of the larger brown algae at 15–20 fathoms (*c.*27–36 m) left an almost pure vegetation of Florideae with some green and blue-green algae. That we to some extent agree with this will be clear from the appropriate sections of the results presented earlier, although the nature of the Floridean vegetation that persists at depths below the laminarian 'forest' fringe shows some bias different to that present at similar depths elsewhere to the south in the eastern Atlantic. Much descriptive literature for the subtidal of the overall region now exists (e.g. Tittley *et al.*, 1977; Price & Tittley, 1978; Hiscock & Mitchell, 1980) and tends to emphasize the often filamentous nature of the red algal species that persist in/below the forest fringes of *Laminaria hyperborea*. By contrast, the characterizing Rhodophyta of Faroese depths are predominantly crustose, with locally dense clumps of erect forms that are largely broad and flat, or in which the filamentous construction is not obvious. Brown and green algae present similarly are rarely of clear filamentous form.

Apart from the over-riding depth limitations imposed on photosynthetic algae by the characteristics of light penetration into water, the limiting factor in the Faroes appears to be the physical nature of the substrate. A perceptive but very general statement on this was made by Børgesen (1905: 706). Characteristics of local and wider water-movement and the area configuration are primary factors in the local condition of substrata; detrital conditions tend not to be present where water-movement directly affects bottom circumstances in the absence of protective configuration. The resultant physical nature of the local substrata imposes limitations and floristic changes within depths at which light characteristics and penetration would be adequate to support growth.

Comparative observations made in the subtidal of the small cove immediately north of the Hoyvík transect area (station 19), for example, revealed that well-developed patches, to 5 m or so across, of coarse stones in the centre of the cove bore flora very different from the bedrock fringes at similar depths. No *Laminaria hyperborea* occurred on the stony patches; at depths of some 5–6 m, intermixtures of well-developed and fertile *Laminaria saccharina* and *Alaria* grew on the stones, with *Polysiphonia urceolata* on larger stones. Bedrock fringes at that location bore the usual strong growths of *Laminaria hyperborea*, with underflora of *Desmarestia viridis, Desmarestia aculeata,* and luxuriant *Chaetomorpha melagonium,* some of which latter was also epiphytic on lower stipes of *L. hyperborea*. Similarly, in the cove to the south of the transect area, the centre presented an equal balance of bedrock and frequent sand patches. Bedrock bore the usual *Laminaria hyperborea* canopy flora, whilst stones and small boulders embedded in the sand bore *Furcellaria lumbricalis, Ahnfeltia plicata, Chaetomorpha melagonium* and *Membranoptera alata*.

The sand itself of the patches within that cove did not bear flora and was clearly of too great a depth for scour- or burial-resistant macroflora to anchor on base-rock or larger fragments and grow through the overlying detritus. There is, in fact, little evidence on the Faroes of significant benthic macroalgal presence where widespread detrital conditions pertain in depths of 10 m or more, unless such conditions are locally patchy and shallowly abut firm rock substrata or are overlain by tolerably stable stones and boulders. Even this latter situation occasionally demonstrates absence of macroalgae, as at station 29 (near Stakkur, Streymoy) where a near vertical cliff descended to 23 m, levelling off to a rough boulder-strewn bottom. The boulder bottom showed no evidence of macroalgae, even the usually widespread crusts of *Cruoria pellita* and the Lithothamnia being absent. Factors other than the nature of the substrate may in this case also have been operating, since there was some evidence of similar macroalgal absence from the basal 2–3 m of the abutting near-vertical cliff.

Although not so in the above case, one of the additional factors that can reduce density of or eliminate growths from the macroalgae of the bottom of coastal slopes, or from flatter areas and gentle gradients within those slopes, is cropping by subtidal marine invertebrates. Examples where invertebrates were noted in considerable abundance include stations 19, the outer end of the head transect at Hoyvík, where *Echinus* and brittle-stars were major characteristics of the biota, and 25, the area of fast current-flow under the middle span of Sundini bridge, where erect underflora and epiphytes were few to absent, crusts (Lithothamnia, including *Lithothamnion glaciale, Pseudolithoderma,* and *Peyssonnelia*) covered the basal stones, and *Echinus,* in fair abundance, *Asterias rubens* and other asteroids were widespread. The transect outer end at station 19 showed no obvious evidence of cropping of the macroalgae that *were* present, although epiphytes on the vigorous *L. hyperborea* there were less dense and individually larger than elsewhere along the transect, perhaps reflecting some control of growth density through browsing. It is not clear to what extent conditions at station 25 reflect the invertebrate activity, but evidence that it does is highly suggestive. Similar correlation appears to apply near Jøkilsgjógv, Kollafjørdur. There, in depths between 12–18 m, small stones stabilized on the surface of muddy/sandy detritus were entirely bare of erect algae, and holothurians, brittle-stars and some *Alcyonidium* occupied considerable space over the whole substrate. The stones and *Modiolus* shells present bore crusts of *Pseudolithoderma* and *Lithothamnion glaciale*.

Invertebrate occupation of space, as opposed to eating habits, is also very disruptive of algal presence and distribution on occasion. Unusual tolerance of invertebrate space-occupation on the part of certain algae may explain the sponge-algal relationships referred to earlier. At station 44 (north side of Fugloy), the horizontal and gently-sloping surfaces of very large boulders either on bedrock or on other boulders embedded in blackish sandy gravel were extensively covered by locally dense populations of *Balanus crenulatus* at depths between 20–29 m. In patches, the coverage by barnacles was 100%. At these depths, the subtidal around the Faroes generally shows coverage of firm rocky surfaces by crustose forms. Although the quicker-growing amongst the usual crusts (*Pseudolithoderma extensum, Cruoria pellita*) were still patchily present on available space in these depths at station 44, there was a noticeable absence of the usually widespread Lithothamnia.

Evidence from elsewhere (station 34, Kalsoyarfjørður, west Kunoy) suggests that unusual density of *Laminaria hyperborea*, very large individually and with very strong stipes, may also adversely affect the presence and distribution of crustose forms in the underflora. At the full density of the forest, between 8–16 m depths in this case, the stable boulders over detritus forming much of the available substrate bore very few crusts compared to the usual conditions, a probable result of outshading by the *Laminaria hyperborea* canopy.

Light, an adequate substrate, tolerable levels of or no invertebrate cropping or space-occupation, and tolerable space competition from other algae, are clearly primary ecological factors controlling the presence and distribution of subordinate algae, be they present as epiphytes on canopy flora or as epilithic/epizoic underflora. Levels of moisture retention or other resistance to drying are also important in the intertidal, although not so in the subtidal. Subtidal fringe epiphytes and underflora require tolerance of the 'moisture-regime' irregularly there applying, but more importantly too of the characteristics of water-movement in that stressful situation. From the data presented (Table 4; also sections 4(i) and 4(ii)), many Faroese species have a wide tolerance-spectrum that enables them to colonize as subordinate flora (epiphytic or underflora) over considerable vertical amplitude from mid-intertidal, through the subtidal fringe and into considerable depths (often below significant laminarian forest growths) of the true subtidal. But what precisely is it that determines this wide distribution and what is the significance? In detail, we often simply do not know. Børgesen (1905: 708 and 757) made general statements regarding ecological requirements and the differences between conditions experienced by canopy flora and by their subordinate epiphytic or underflora, without approaching many of the significant and interesting ecological questions that automatically arise. He commented throughout his 1905 work on the species present in the subordinate flora, particularly as regards intertidal fucoids, *Himanthalia,* and the laminarians.

Laminaria hyperborea was the subject of an interesting analysis (1905: 757) of the stipe and holdfast epiphytes. The study of sequence down the stipes, detailed and attributed to light requirements by Børgesen, was repeated to some extent (at station 38) during our work but, apart from the very general tendency for *Callophyllis laciniata, C. cristata,* and *Fimbrifolium dichotomum* to occupy positions basally on the stipe and over the holdfast (also noted by Rex, 1970, for the first two species), we were unable to confirm Børgesen's findings. *Polysiphonia urceolata,* for example, was as likely to be found basal to the stipe or on the holdfast 'crampons' as it was distal on the stipe. *Palmaria palmata,* mentioned by Børgesen (1905: 754) for old *Alaria* stipes and suggested as probably common on *Laminaria hyperborea* laminae in spring, was not listed by him in his stipe treatment (1905: 757), although he did (1905: 755) comment on the shallow-water *L. hyperborea* populations with laminae partly revealed at low water, continuing

'It is here that the above-mentioned epiphytical *Rhodymenia*-vegetation has its habitat.' This is ambiguous, leaving considerable doubt as to whether *Palmaria* was detected by him on laminae or on stipes. Yet in our studies, as in that of Rex (1970), *Palmaria* was one of the most common stipe epiphytes. We have to regard Børgesen's treatments in this context as over-generalization.

Clearly, there remains to be carried out a great deal of fundamental research on spore production, viability, phenology, biochemical environmental reactions as to attachment with permanency or failure in that, reproductive element carriage characteristics in the water medium, reattachment phenomena, and a host of biological characteristics of settlement and population formation, before conclusions drawn from field observations on natural distribution and populations of epiphytes/epilithic flora are more than simply informed speculation. We gain the impression from the Faroes observations and from work elsewhere that the situation is one of self-perpetuating patterns of distribution in particular conditions once an adequate foothold has been gained and while the conditions do not alter. With certain manifest exceptions (e.g. *Polysiphonia lanosa* and its usual restriction to two host species), the more vigorous subordinate taxa in their usual/optimal vegetative and reproductive field-states settle fairly indiscriminately on whatever acceptable or tolerated surfaces present themselves at the right times and places; the balance of resultant recognized 'choice'-pattern in distribution seems to relate more to chance comparability of depth distribution of hosts, to local current patterns and configurations, and to reproductive element carriage and viability (or to the distinguishing of different morphologies adopted by probably single biological subordinate species according to growth in one or another habitat) than ever it does to real restrictions derived from growth requirements for particular bearing surfaces.

Even with this set of reservations on available information, there remain several taxa for which there are obvious comparative anomalies in the extent of recording, or in the *actual* absence/presence, between data in Børgesen, in Rex, in Holt, and our own studies. An outstanding case in point is that of *Dilsea carnosa,* the presence of which on the Faroes was dismissed as error by Rostrup and by Børgesen (1902: 397), despite the existence of an earlier record by P. A. Holm (detailed reference to that record being given in Børgesen, *loc. cit.*). Rex (1970) re-established firmly the presence on the islands, commenting that Børgesen was himself here in error since the species was frequent in the sublittoral, as underflora to *Laminaria hyperborea* in depth of 3–5 m (Hoyvík) and 3–8 m (Borðan, on Nólsoy). We detected *Dilsea carnosa* extensively, in situations from lower intertidal deep shaded pools down to 30 m in the subtidal, at 21 sites; always epilithic, the species grew as underflora to *Laminaria hyperborea* (mostly), *L. digitata*, and *Alaria.* Because of the extent of his dredging activities, it is surprising that Børgesen, despite lacking direct observation from underwater work, saw no reason to accept the presence of *D. carnosa* on the Faroes. Does this species there undergo periodic, perhaps irregular, immense and widespread fluctuations in biomass?

A similar, if less impressive, situation exists with *Desmarestia ligulata*, which is certainly much rarer than *Dilsea*. Børgesen (1902) recorded the species as a few specimens from few localities, commenting that extensive growths could somewhere be expected because of frequency in the drift. We saw no material in the drift and our sole record of *Desmarestia ligulata* was as a single plant on rock of a vertical face in 10–12 m at station 29 (near Stakkur). Rex (1970) recorded the plant in the sublittoral at Hoyvík, moderately frequently, on stipes of *Laminaria hyperborea,* a not impossible but fairly infrequently encountered habitat for this species. Holt (1975) did not mention *Desmarestia ligulata*. It is interesting that whereas we recorded *D. ligulata* but once and the other species (*D. aculeata, D. viridis*) in the genus frequently, but almost exclusively epilithic as underflora to *Laminaria hyperborea* or in depths (both to 29 m) below the lower limits of the latter, Rex (1970) recorded all three *Desmarestia* species as either moderately frequent (*D. ligulata*) or frequent (*D. aculeata, D. viridis*), and always on *Laminaria hyperborea* stipes.

The presence of *Alaria* in its usual fringing position along the water-line on firm rock (e.g. at station 19) is clear from the presented profiles. This organism, the subtidal fringe and shallow subtidal dominant in a wide variety of conditions on the Faroes, demonstrated in the island group some differences of detailed distribution from that suggested by earlier authors. *Alaria,* not a particularly reliable indicator for the Faroes of the open-water exposure to wave-action that it most successfully characterizes in, for example, southern and western Britain, did not in our work commonly reveal the continuous distribution from minimum to maximum depths exploited that would be expected from some of Børgesen's statements. As indicated for the cove to the north of the station 19 transect, deeper populations located tended to be outliers, not in contact with lower fringes of the full *Alaria* band at the shallower depths; these and other *Alaria* outliers seemed often to be involved with substrata that did not support the usual *Laminaria hyperborea* populations. This is a point that was not adequately pursued in Børgesen's text; nor did the latter comment on the fact that the lower populations were frequently composed only of sporelings. The significance of the latter is not clear; seasonal observations of the progress of the populations is required. In some cases, the often sparse deeper populations may never attain vegetative or reproductive maturity.

Cladostephus spongiosus is a remarkably common species in areas to the south of the Faroes in the north-east Atlantic; it occurs both intertidally, in standing water and damp places, and subtidally. Børgesen (1902: 434) reported it locally at Gjógv (our station 31) on the promontory examined in some detail during the present studies, but we were unable to detect material anywhere (there or elsewhere) in the often likely conditions. It is curious that the species has only very recently (Munda, 1981) been recorded in print for Iceland, another area for which one would have expected there to be previous records. Perhaps this organism is another that shows phasic or irregular range expansion and contraction, especially detectable at range peripheries. Previous restricted presence in the Faroes may, despite no published Icelandic records then, have been paralleled by its local distribution in Iceland. Both island groups may be showing the same pattern, simply not previously noted in Iceland, or the alga may have taken some time to progress from the Faroes to Iceland, meanwhile not being even locally particularly consistent on the former due to such factors as stress of conditions at apparent range peripheries. Finds on both Iceland and the Faroes were of sterile material only.

We were able to establish a further unequivocal new record for the island group, in the form of the '*Trailliella*' phase (tetrasporophyte) of *Bonnemaisonia hamifera*. Details are presented in Table 4, but it is worth emphasizing here that open-shore lower intertidal standing waters and sheltered subtidal fjordic conditions, coupled with an artificial substrate (polythene bristles), were both involved. It is very probable that this organism is or will be more widespread and is in an actively spreading phase, since it has only comparatively recently been recorded from Norway (Printz, 1952), Iceland (Munda, 1978), and adjacent regions (e.g. the Shetlands—Irvine *et al.*, 1975). It would be reasonable to expect the appearance shortly of the gametophyte-phase, *Bonnemaisonia hamifera,* on the Faroes. Lye (1965) recorded this phase as new to Scandinavia some years after the initial report of its tetrasporophyte; Kornmann & Sahling (1962; 1977) similarly established the presence of the gametophyte on Helgoland, where previously only the tetrasporophyte was known.

It is curious that the northern species *Turnerella pennyi* was not unequivocally detected at any time during our work period on the islands. Field records for that species established for three stations all emerged on checking as young *Dilsea carnosa,* which seems readily confused with *Turnerella* when being observed under water. South *et al.* (1972) outlined the synonymy and distribution for north Atlantic forms in the genus, concluding that despite various names applied *T. pennyi* is the only species present in the Arctic and Sub-Arctic, south to Iceland and east Greenland.

A conversion of the subtidal growth limits presented by Børgesen (1902; 1905) for many of the benthic algae of the Faroes from the original fathoms into metric equivalents reveals that in some cases the stated maximum depths exceed those detected by us during the present survey. In part, this could well be due to logistic (scuba) limitations that restricted the depths examined, but in many cases (see the site list for examples) the necessary firm substrate disappeared beneath detritus well above these depths. In other cases (e.g. station 29), available substrate was apparently entirely adequate to support a 'normal' benthic flora, but the latter demonstrated lower limits well above both lower dive limits and the maximum depth limits for particular species, as stated by Børgesen (1902). Although there are stations (e.g. 12, 30, 44) at which some algae grew down beyond the already unusually deep dive limits, it is clear that the limits representing the most usual situations could usefully be stated as the normal range for the organism concerned, with the unusual deeper occasional limits being stated as such, much as we have done for certain occurrences of the *Laminaria hyperborea* forest. Additional factors in the differences between lower limits perceived may rest in the fact that Børgesen's subtidal data were derived largely from dredging, rather than from scuba work. The difficulties inherent to accurate estimation of dredging depths when (i) the angle of the cable used is not perpendicular, and (ii) the dredge may in descending or ascending have passed over other shallower surfaces from which plants may derive, are well known.

No doubt in a few cases Børgesen was correct and our recorded maximum depths for taxa are possibly underestimated as extreme tolerance limits; in others, however, consistency of species limits noted by scuba observation during our work scheme (see Table 4) would suggest that re-assessment of earlier results is required. A comparison of details presented for species in the tables (especially Table 4) with those given in his species entries by Børgesen (1902) will demonstrate instances of both the above, and we accordingly do not reiterate these data here.

iii. The intertidal

The generalities of the intertidal situation, which as indicated elsewhere are aside from the main aims of the present paper, are not covered here. In order to avoid unnecessary repetition and to establish variations detected by us from previous data, the presentation above of intertidal results was largely comparative and discursive, predominantly in regard to Børgesen's earlier studies. No further comparative discussion is therefore presented. It is worth emphasizing that in line with existing use of detailed observations on ecology and biology of certain intertidal Ceramiaceae, indicated elsewhere, further similar data will subsequently be employed in more detailed and integrated analysis.

One apparently rare species worthy of mention for the Faroese intertidal is *Laurencia pinnatifida,* which we were unable to record from anywhere in the island group. Although Børgesen (1902: 371) commented that it was then very rare, he was at least able to detect it covering the bottom of a high level rock-pool between Tórshavn and Hoyvík, Streymoy. This stretch of coastline was examined in some detail during the present work, both for general collections and during transect reading, and the species is unlikely to have been overlooked there. We were not able to fit in visits to the localities on Suduroy for which Børgesen also indicated records of this species.

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Aino M. Henssen & Peter W. James

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The lichen genus *Steinera*

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Synopsis

A revision of the genus *Steinera* Zahlbr. is presented, based on *S. glaucella* (Tuck.) Dodge and four new taxa, *S. polymorpha* P. James & Henssen, *S. radiata* subsp. *radiata* P. James & Henssen, *S. radiata* subsp. *aucklandica* P. James & Henssen, and *S. sorediata* P. James & Henssen. A fifth species, *S. werthii* Zahlbr., may also be recognized, but unfortunately the original material appears to have been destroyed. A detailed study of the ontogeny of the asocarp shows that the genus should be transferred to the Coccocarpiaceae. Its relation to the other genera in this family, namely *Coccocarpia, Peltularia,* and *Spilonema*, is discussed.

1. Historical background

The genus *Steinera* was described by Zahlbruckner (1906: 41). It was based on Nylander's name *Amphidium molybdoplaca* (= *Steinera glaucella* (Tuck.) Dodge) published, with a description, by Crombie (1875: 333 '*molybdophæum*') of material collected by A. E. Eaton from Kerguelen Island during the voyage of the Venus Transit Expedition. However, from Zahlbruckner's diagnosis there is no evidence that he examined the original material seen by Nylander, now in the herbarium in H (Nyl. no. 42805), or the related collections in BM. Nor is there any evidence that the material of Tuckermann's *Pannaria glaucella,* cited by Zahlbruckner (1906: 43) as a synonym of *Steinera molybdoplaca*, was referred to. It is therefore probable that the diagnosis of

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the new genus was based on Crombie's original description and new, and now lost, material of the genus collected by Urbansky and Werth from Kerguelen Island on the Deutsche Südpolar-Expedition of 1901 to 1903. Although Zahlbruckner includes no description of Urbansky's material which he named as *S. molybdoplaca,* his illustration (1906: pl 4, fig. 14) of three-septate spores is in good accord with *S. molybdoplaca* as understood by Nylander. In the same paper Zahlbruckner (1906: 43) describes a new species, *S. werthii,* which is notable for its small size ('usque 10 mm. latas'), the squamulose centre of the thallus, the small, one-septate spores, and pycnidia with endobasidial conidiophores. From the illustrations (1906: p. 4, figs. 1–12) the characteristic thallus anatomy of more or less vertically aligned fascicles of the phycobiont interspersed with hyphal filaments indicates that *S. werthii* was obviously correctly placed in *Steinera*. Unfortunately, we were unable to verify Zahlbruckner's account, since material of either species could not be located; it is presumed that both specimens were destroyed in Berlin in 1943; *S. werthii* may be related to *S. radiata*.

In describing his new genus Zahlbruckner (1906) refers to the phycobiont of *Steinera* as having 'gonidiis calothricoideis' and makes a direct comparison with the algae in '*Thamnidium willeyi*' (now *Lichina willeyi* (Tuck.) Henssen), a provisional name used by Schwendener (1869) in his important treatise on lichen algae. According to Zahlbruckner the phycobiont of *Steinera*, which is described as filamentous with basal heterocysts, only differs from that described for '*Thamnidium willeyi*' in not having tapered ends to the filaments. Since Zahlbruckner (1906) gave no account of the now lost material collected by Urbansky which he named as *S. molybdoplaca* it is not certain whether, in fact, he examined a different taxon from this species which did not contain *Nostoc*, the phycobiont definitely present in the type specimen of this species described by Crombie. However, since the illustrations of the spores of the Urbansky gathering (1906: pl. 4, fig. 14) are identical with those of *S. glaucella,* it is possible that Zahlbruckner was mistaken in his identification of the phycobiont. Zahlbruckner's illustration in Engler & Prantl (1926: Figs 76 A–C) is probably based on Urbansky's material but does little to resolve the problem, for, although it conveys the characteristic radiate arrangement of the hyphae and algal filaments in the genus, the identity of the phycobiont remains obscure. Whilst the individual algal cells are rounded and bead-like as in *Nostoc*, they are too large, in relation to the adjacent hyphal cells, to belong to that genus. Furthermore, the algae are distributed in solitary filaments, the arrangement characteristic of members of the *Rivulariaceae* (Figs 12A–B, 23A–B) and not in fascicles – a notable feature of the arrangement of the *Nostoc* chains in the genus (Figs 17A–C, 19C, 21A–B). The true position of the heterocysts cannot be accurately determined from the illustrations.

A third, and sterile, species, *Steinera neozelandica*, was added to the genus by Dodge (1971). Anatomical investigation of an isotype of this species, from New Zealand, Canterbury, Woolshed Hill, off rock along screefield, February 1958, *L. Visch 78* (CHR), reveals that this taxon belongs to the *Pannaria—Parmeliella*—complex, and is therefore not considered further in this account; material of *Steinera nigra* Dodge (Dodge, 1948 p. 461) has not been made available to us for study.

The discovery of three new species of *Steinera* presented here has provided important information on the characteristics and delimitation of this hitherto poorly understood genus.

2. Ontogeny of the ascocarp and systematic position of the genus

Introduction

As a result of his interpretation of the phycobiont in *Steinera* the genus was included in the Lichinaceae by Zahlbruckner (1906). Dodge (1948), whilst retaining *Steinera* in its original family, suggested a closer affinity with the Peltigeraceae, especially with the genus *Solorina*. Although the characteristic form of the thallus of *Steinera* bears some superficial resemblance to certain members of the Lichinaceae, as for instance, *Porocyphus effiguratus* Henssen (Henssen, 1974), ontogenetical studies indicate that the true affinities of the genus lie with the Coccocarpiaceae (Henssen, 1975; Keuck, 1977). The most recent delimitation of the Coccocarpiaceae (Henssen *et al.,* 1981) includes lichens with filamentous (*Spilonema*), foliose (*Coccocarpia*), peltate (*Peltularia*), and placoid (*Steinera*) habit. The unifying feature of this seemingly disparate assemblage of genera lies in their unique ontogeny (see below), the considerable differences in the filamentous and ±foliose morphology being due to the respective phycobionts. The filamentous genus *Spilonema* has species of *Stigonema* or *Hyphomorpha* as symbiotic algae (Henssen 1963, 1981) while in the non-filamentous genera the phycobionts are species of *Scytonema, Nostoc,* or unidentified genera of the Rivulariaceae. It seems that filamentous blue–green algae with true branching exert a greater influence on thallus morphology.

In its anatomy and developmental morphology of the ascocarp, *Steinera* most closely corresponds to the monotypic genus *Peltularia.* Both genera are restricted to the Southern Hemisphere and may have evolved from a common ancestor.

Ascocarp ontogeny in the Coccocarpiaceae

In the Coccocarpiaceae the apothecia develop in a unique way from the aggregation of short cells which are continuously supplemented by the adjacent hyphae of the thallus. True paraphyses, the only type of interascal filaments developed in the family, arise by elongation of the marginal cells of the ascocarp primordium (Henssen, 1963; Henssen & Jahns, 1973; Keuck, 1977; Henssen *et al.*, 1981).

In *Spilonema* (Fig. 1 A–D) the primordium includes straight ascogonia. The apothecia, which are relatively simple, are convex from the beginning and lack a well defined excipulum. In the species of *Coccocarpia* examined, the apothecia are closely appressed to the thallus and spread laterally; in this genus the subhymenium tends to develop into a stipe (Fig. 2A–D). Unlike *Spilonema*, algal cells are introduced at an early stage of development of the primordial tissue as well as in the production of the subhymenium of the maturing apothecium. The well developed excipulum is composed of radiating hyphae (Fig. 2D). In *Spilonema* and *Coccocarpia* the asci tend to be distributed in groups; the paraphyses are relatively thick, partly branched in the upper part and terminate in tapered or enlarged apical cells.

In *Peltularia gyrophoroides* (Räsänen) R. Sant. (H—holotype) the generative tissue of the primordium is composed of less regularly arranged hyphae than those occurring in the primordia of either *Spilonema* or *Coccocarpia* (Fig. 3A). In this genus the subhymenial layers are very clearly defined from the surrounding laxer network of the medullary hyphae (Fig. 3B–C). In later stages the hypothecium *sensu stricto* becomes clearly delimited from the formative tissue below (Fig. 3D). The latter gives rise to an annular excipulum surrounding the hymenium. In spite of the lateral extension of the apothecia which is similar to that in *Coccocarpia*, in *Peltularia* the excipulum remains rather delimited (Fig. 3E). Algal cells are incorporated by the formation of the generative tissue of the primordium as well as by the subsequent enlargement of the subhymenium due to the addition of supplementary cells from the adjacent hyphae (Fig. 3B–C). In contrast to *Spilonema* and *Coccocarpia* a thalline margin of a secondary nature occurs, similar to that in the Pannariaceae (Henssen, 1969; Henssen *et al.*, 1981), and as in that family, the upgrowth of the hyphae surrounding the ascocarp includes filaments of the phycobiont. In the final stage of development the thalline margin becomes recurved towards the surface of the thallus as a result of expansion of the developing excipulum (Fig. 3D–E).

In the genus *Steinera* the ontogeny is diverse and development in certain species tends to amplify particular features outlined above for the other genera of the Coccocarpiaceae. In the type species of the genus, *S. glaucella*, the generative formative layer of the primordium (later becoming the formative tissue) is composed of short-celled, pigmented, vertically aligned hyphae (Figs 4A, 5A). These are densely compacted in the more marginal areas and thus tend to form a cupular, excipulum-like layer surrounding a gradually gelatinised matrix in which the ascogenous hyphae, the first asci and developing true paraphyses, are embedded (Figs 4A–B, 5B–D). The cupular, dark pigmented structure in mature apothecia which surrounds the hymenium (Fig. 5E) is composed of deeply staining hyphae and is actually the outer part of the formative layer which subsequently becomes enlarged by the characteristic method unique to the family, the addition of short cells from the adjacent medullary hyphae. As in *Peltularia* an apothecial margin containing algal filaments is a secondary development but, unlike in that

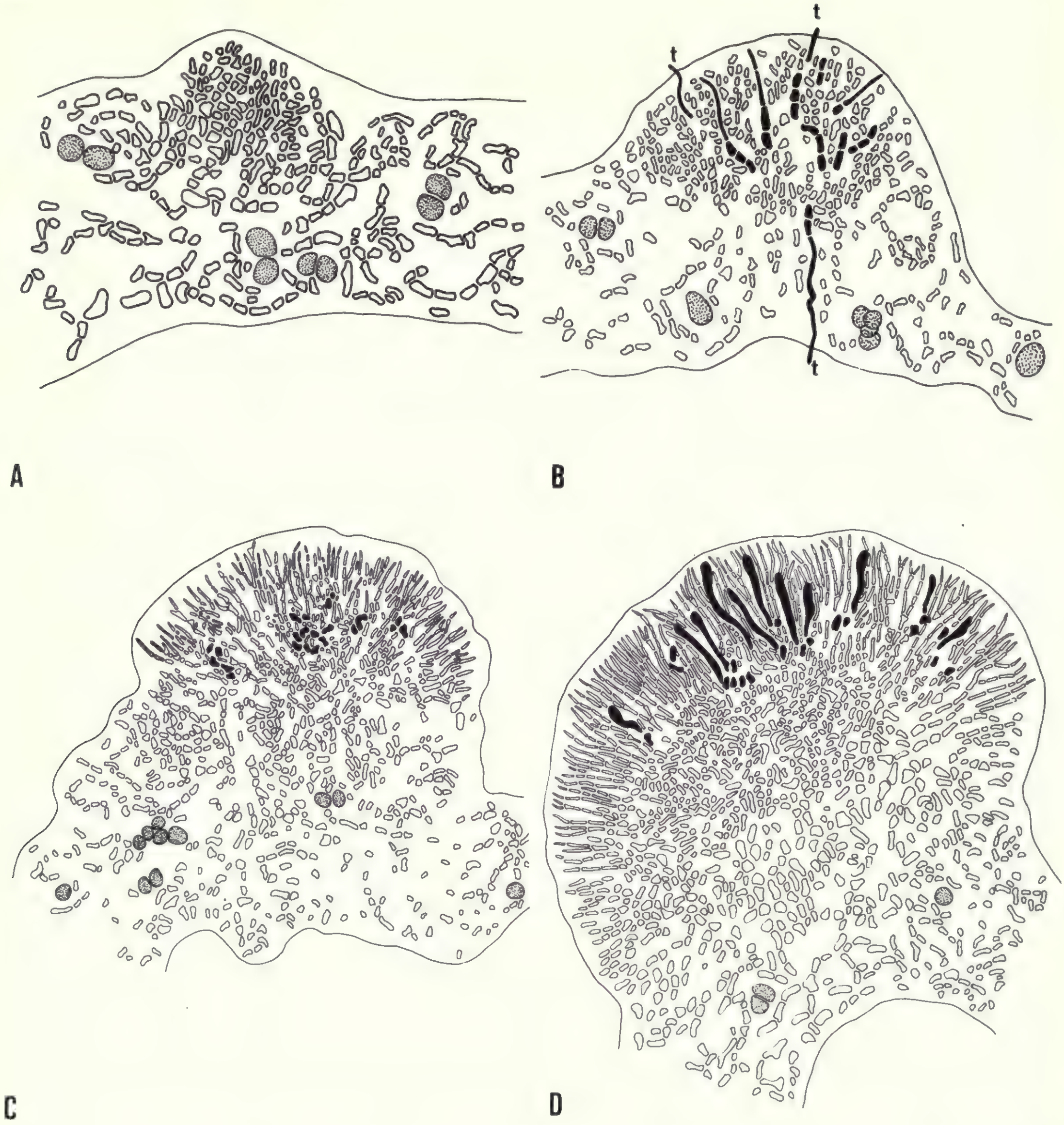

Fig. 1 Development of the ascocarp in *Spilonema paradoxum* Bornet. A Primordium composed of aggregated short cells. B Later stage with straight ascogonia bearing trichogynes (t). C Young apothecium with groups of ascogenous hyphae and paraphyses. D Mature globose apothecium. A–D from Henssen & Jahns (1973).

genus, the inner part of the margo thallinus is lined by an extension of the formative layer (Figs 4C, 6A–B); no true excipulum proprium is developed.

In *Steinera polymorpha* the persistently immersed apothecia are characteristic of the species. Exceptionally, an upgrowth of tissue may occur between contiguous apothecia (Figs 7C, 18B–C) homologous with the marginal structures which surround the apothecia of *S. glaucella*. A cupuliform outer part of the formative layer is similar to and as distinct as that in the latter species (Fig. 7D). The early stages of development may include one or several complexes of ascogenous hyphae (Fig. 7B–C).

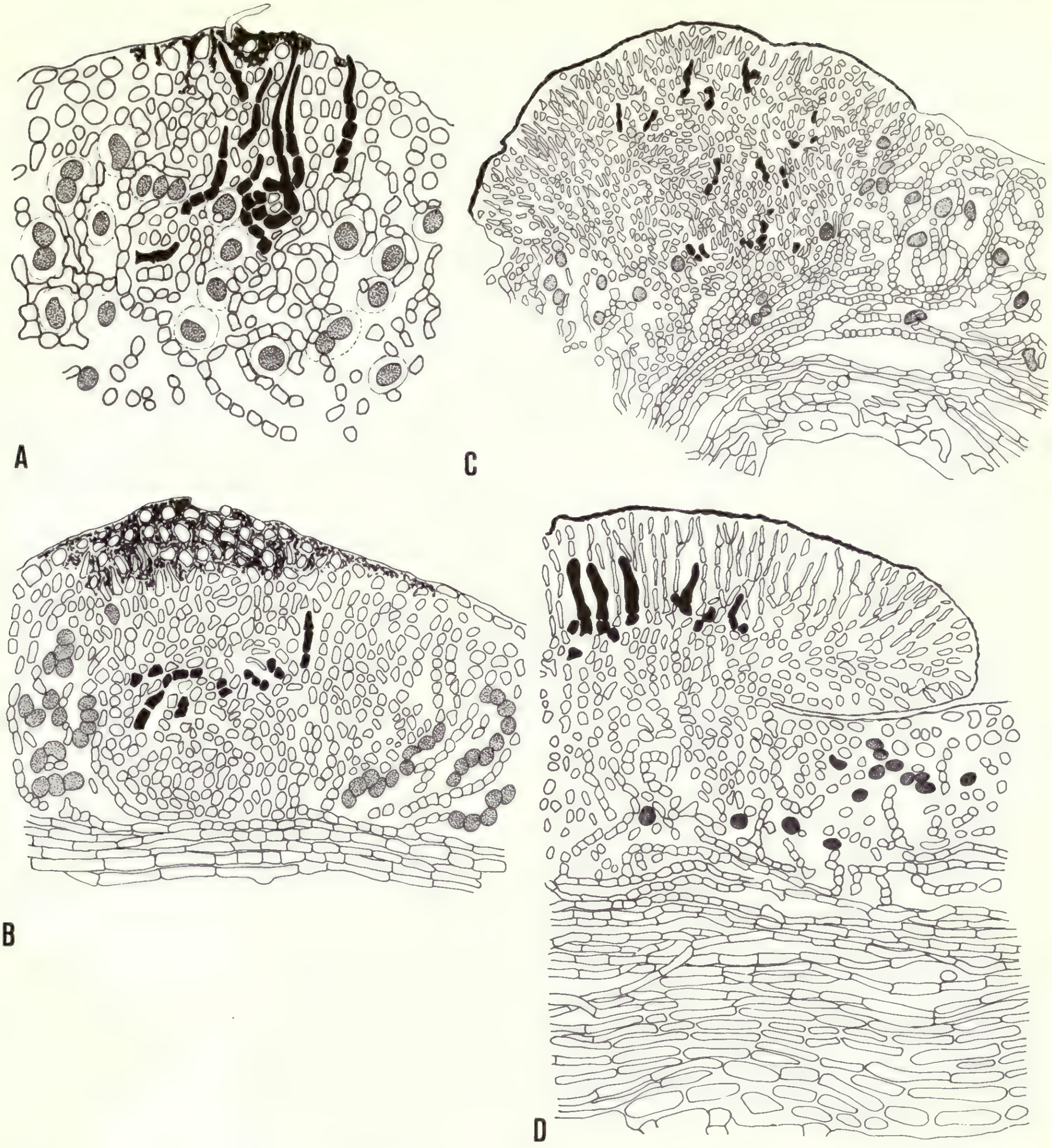

Fig. 2 Development of the ascocarp in *Coccocarpia erythroxyli* (Sprengel) Swinscow & Krog. A Primordium containing ascogonia. B Primordium with ascogenous hyphae embedded within an aggregation of short cells of the generative tissue. C Young apothecium, medullary hyphae breaking up into short cells. D Marginal part of mature apothecium. A–D after Henssen *et al.* (1981).

In *Steinera sorediata* a hemiangiocarpic development is indicated since the hymenium in the young apothecium is covered by thalline tissue (Fig. 8A). However, a detailed study was not possible due to the lack of suitable material. The development of the apothecial margin in *S. sorediata* corresponds to that of *S. glaucella* with the exception that the formative layer is less distinct in the secondarily compound apothecial margin (Fig. 8A–B). The outer thalline part of the margin becomes sorediate; the soredia develop in the same way as on the surface of the thallus.

In *Steinera radiata* the ontogeny of the apothecia differs considerably from the other three

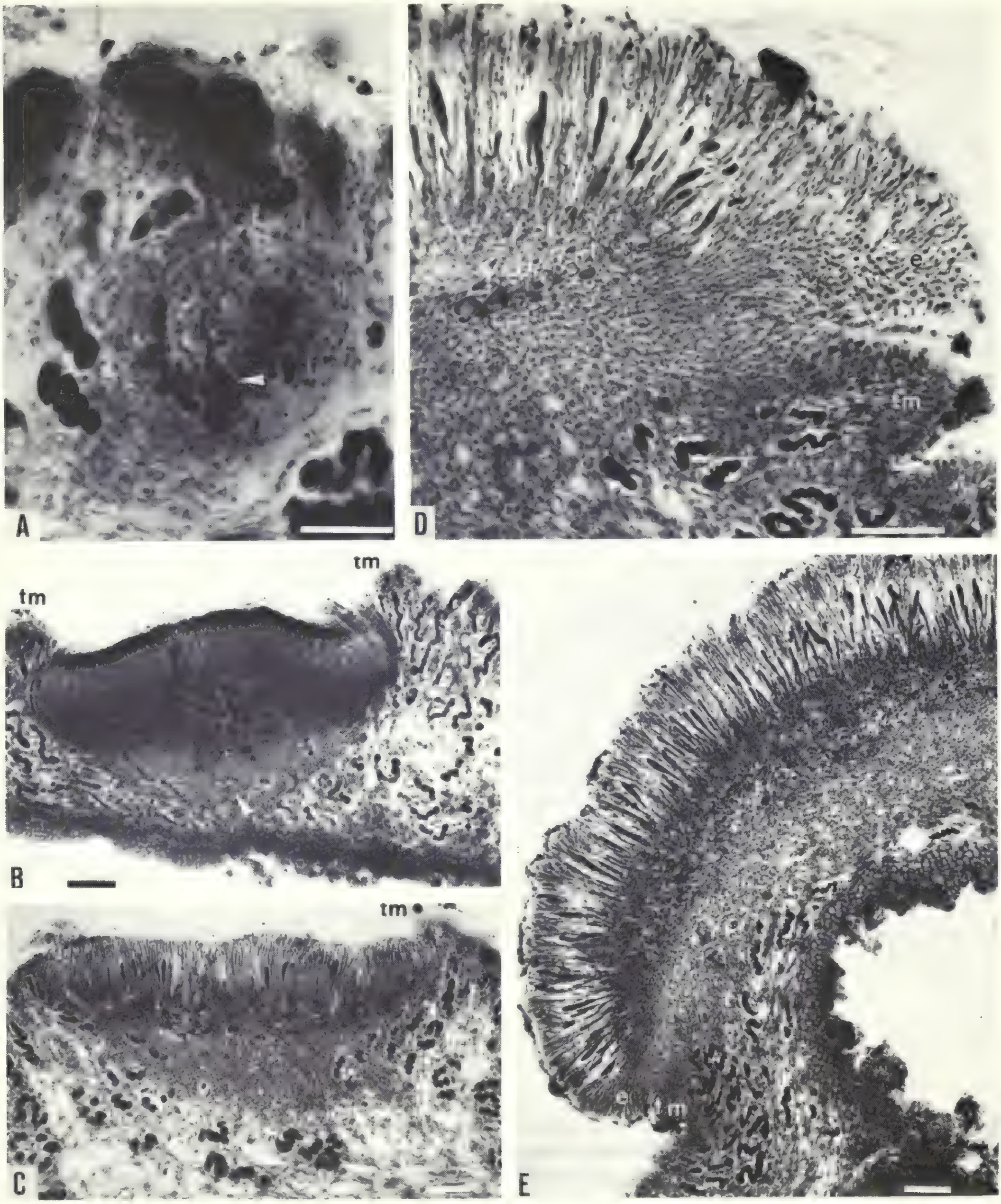

Fig. 3 Development in the ascocarp of *Peltularia gyrophoroides* (Räsänen) R. Sant. (holotype, H). A Generative tissue including ascogenous hyphae and young ascus (arrow). B Section of young apothecium surrounded by a secondarily developed thalline margin (tm), subhymenial cells isodiametric (arrow). C Young apothecium developed within the algal zone of the thallus with an elevated thalline margin (tm) at one side. D Marginal part of old apothecium, thalline margin (tm) reflexed towards the thallus surface by the developing excipulum (e). E Old apothecium with excipulum (e) and inconspicuous thalline margin (tm). B–D after Henssen *et al.* (1981). Scale A = 20 μm; B–E = 50 μm.

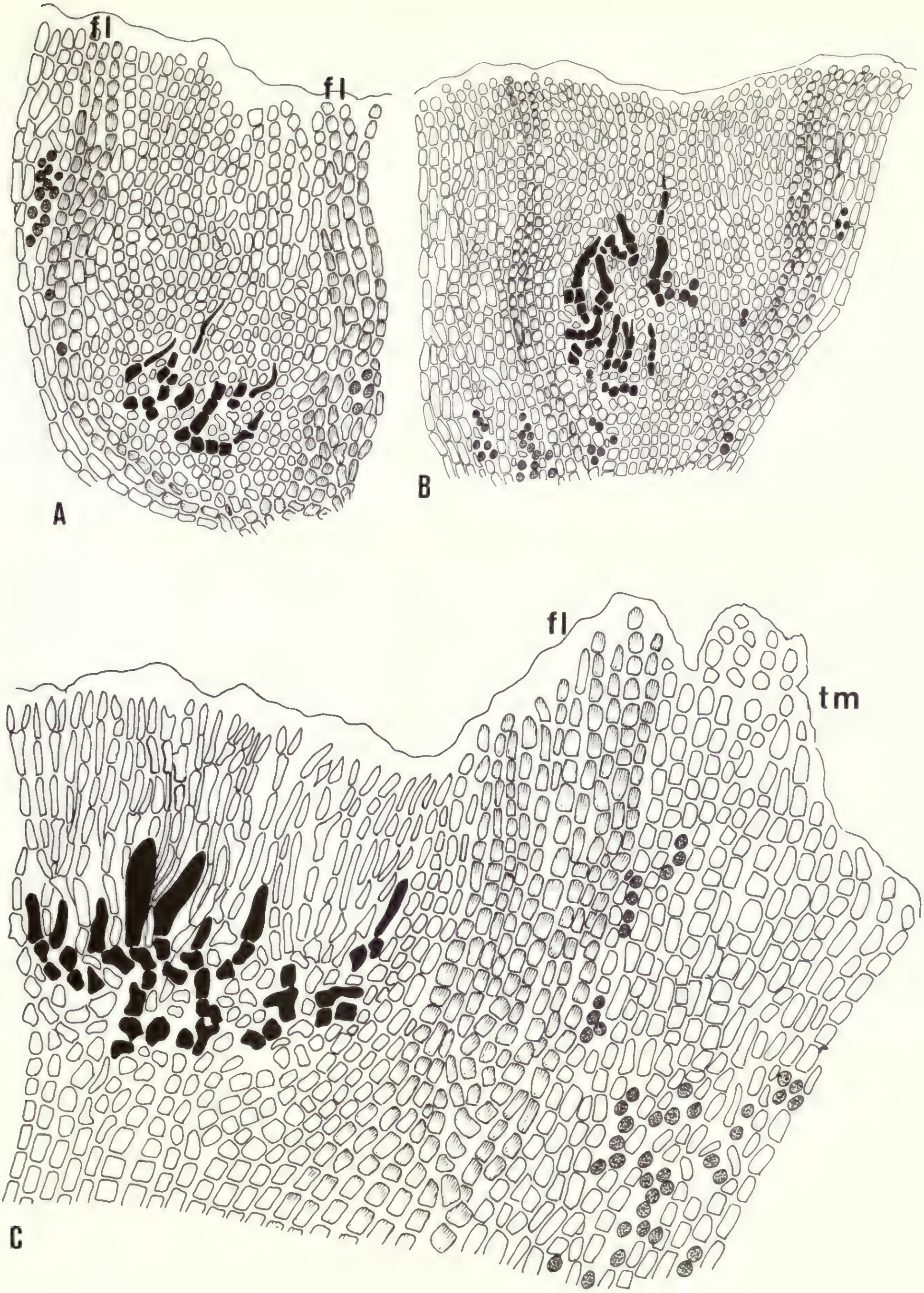

Fig. 4 Development of the ascocarp in *Steinera glaucella*. A Primordium with remnants of ascogonia and trichogynes; note the pigmented cells of the formative layer (fl). B Later stage with ascogenous hyphae and first ascus. C Section of mature apothecium with compound margin composed of pigmented hyphae of the formative layer (fl) and thalline margin (tm). Scale A, C = 50 μm, B = 20 μm.

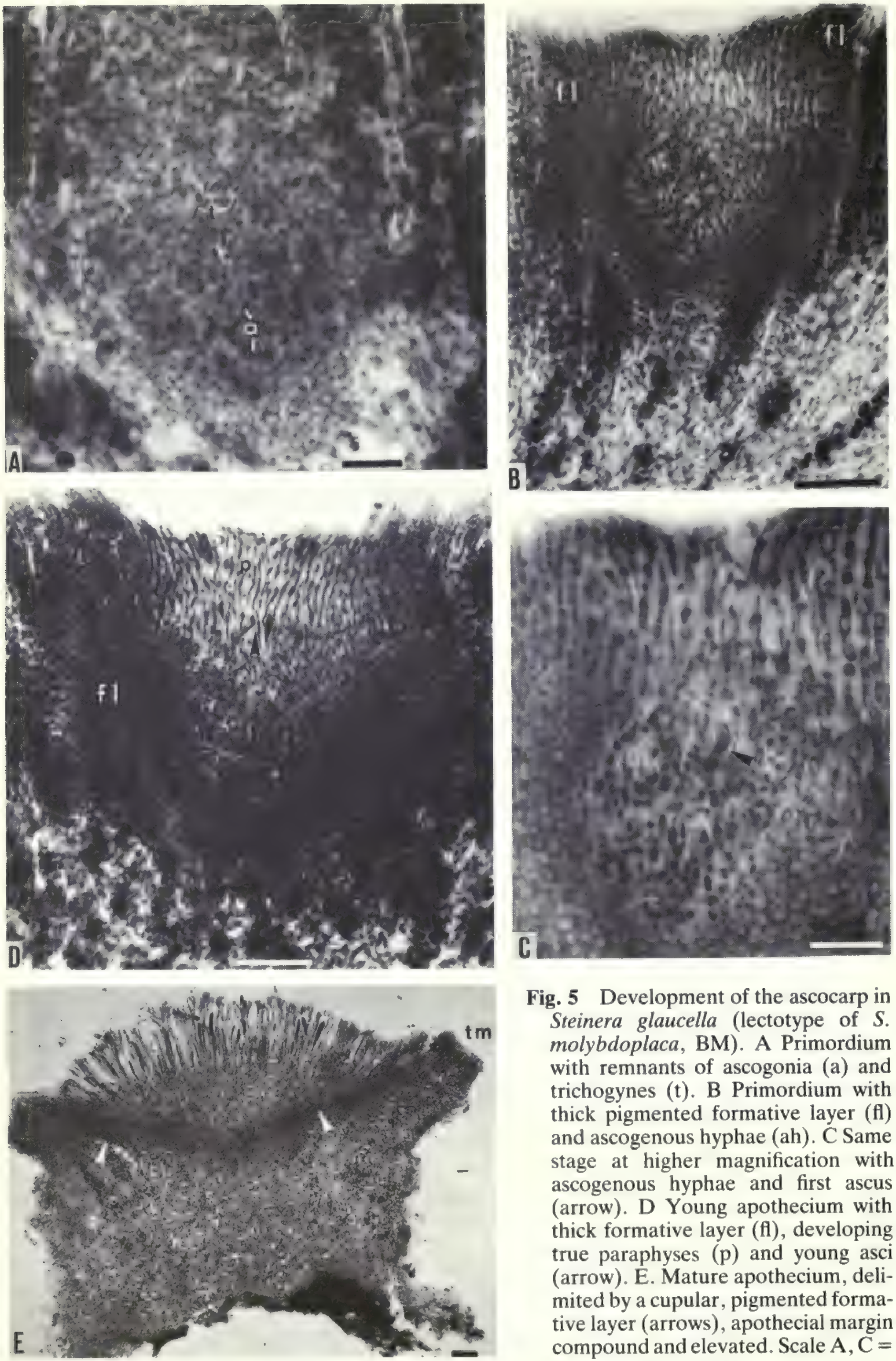

Fig. 5 Development of the ascocarp in *Steinera glaucella* (lectotype of *S. molybdoplaca*, BM). A Primordium with remnants of ascogonia (a) and trichogynes (t). B Primordium with thick pigmented formative layer (fl) and ascogenous hyphae (ah). C Same stage at higher magnification with ascogenous hyphae and first ascus (arrow). D Young apothecium with thick formative layer (fl), developing true paraphyses (p) and young asci (arrow). E. Mature apothecium, delimited by a cupular, pigmented formative layer (arrows), apothecial margin compound and elevated. Scale A, C = 20 μm; B, D, E = 50 μm.

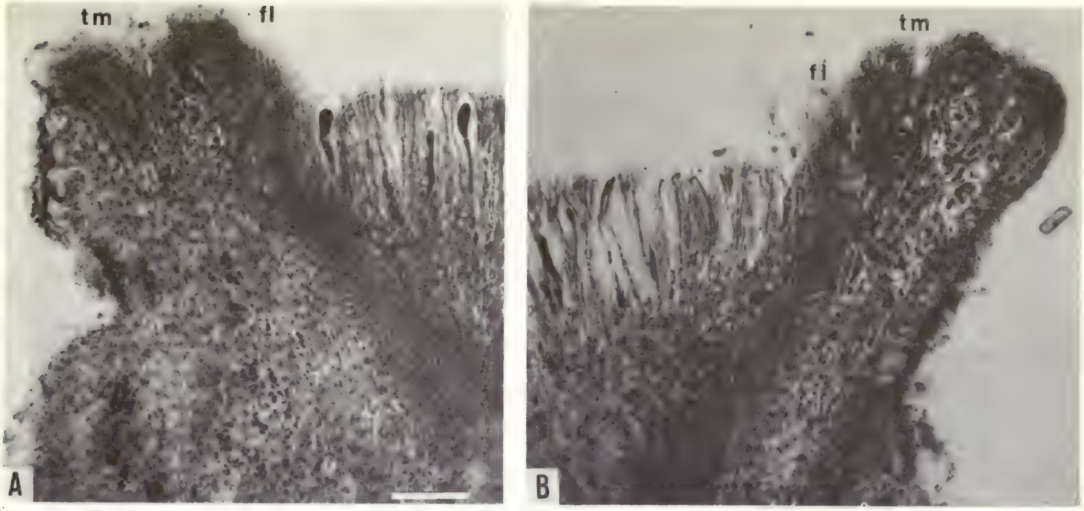

Fig. 6 *Steinera glaucella* (lectotype of *S. molybdoplaca*, BM), secondarily developed apothecial margin composed of thalline margin (tm) and formative layer (fl). Scale = 50 μm.

species of *Steinera*. The initial stage, involving the development of coiled ascogonia with thick trichogynes (Fig. 9A), resemble that in *Coccocarpia erythroxyli* (Sprengel) Swinscow & Krog. Further development of the apothecium is distinctly hemiangiocarpic. The remnants of the overlying thalline tissue is gradually ruptured and pushed back with the ensuing enlargement of the hymenium and subhymenium (Fig. 9C–E). At first the young apothecia are surrounded by the remnants of the thalline tissue, the proper margin at this stage being rudimentary (Fig. 9F). In old apothecia a well developed, annular excipulum proprium with a radiate structure is present which expands laterally obliterating and fusing with the remnants of the adjacent thalline tissue, thus forming a compound proper margin (Figs 9G, 10A–B, 11). During the development the paraphyses have characteristic tapered apices (Fig. 9B) as in *Spilonema* and *Coccocarpia*; eventually the upper parts of the paraphyses in *S. radiata* subsp. *aucklandica* become submoniliform (Figs 13B, 23E).

3. The genus *Steinera* Zahlbr., emend. P. James & Henssen

Thallus placoid, rarely irregular, effigurate, sometimes forming ± regular rosettes, closely appressed to loosely attached. Margin ± lobate, lobes sometimes flabellate, mostly radiating, inner part of the thallus conspicuously rimose-areolate, the entire thallus intersected by deep, radiating and anastomosing fissures. Thallus surface smooth to markedly scabrose, lower surface grey–brown–black, ecorticate. One species sorediate. Phycobiont *Nostoc*, or (in one species) a member of the Rivulariaceae. Thallus medium to thick (<1000 μm), ± homoiomerous, hyphae short-celled, often with fascicles of the phycobiont dispersed in a characteristic radiating, fan-like arrangement which is commonly horizontally aligned near the lower surface, soon becoming vertically orientated above and towards the upper surface. Upper part of thallus with more or less closely packed, isodiametric cells forming a pseudoparenchyma-like tissue.

Apothecia innate and urceolate to emergent and adnate, disc smooth, red–brown to black–brown. Epithecium red–brown to deep brown, not granular, pigment external to the tips of the paraphyses. Paraphyses rarely simple, usually sparingly to richly branched and anastomosing, distinctly septate, sometimes submoniliform towards the apices, apical cell sometimes enlarged, to 9 μm. Asci elongate-ellipsoid to ± cylindrical, with thickened apex (tholus) containing either an amyloid cap or a ring structure. Spores 8 per ascus, simple to multiseptate, colourless, thin-walled, sometimes with one or both ends tapered. Subhymenium well developed, colourless, of short-celled hyphae which often form a basipetal, downward extension into a stipe-like

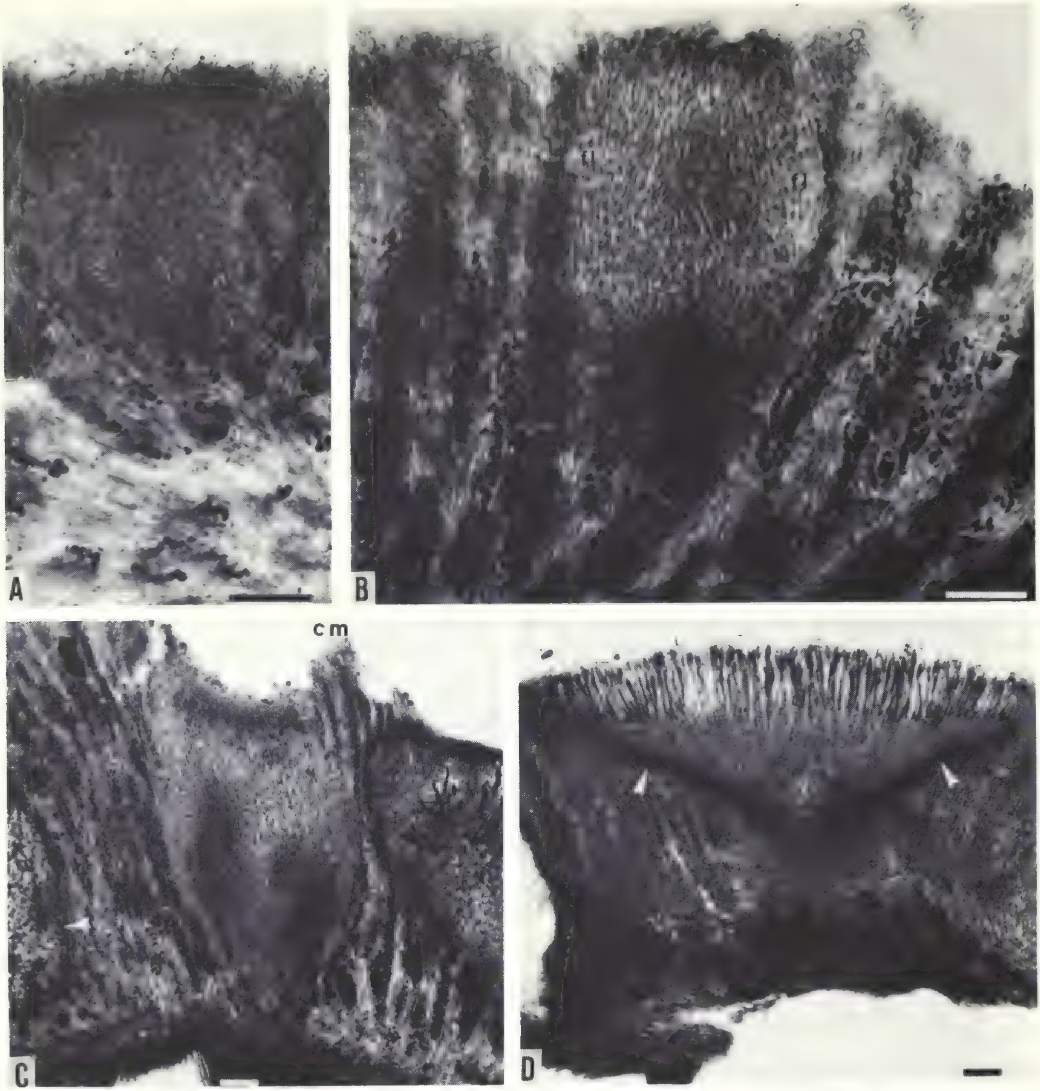

Fig. 7 Development of the ascocarp in *Steinera polymorpha* (holotype, BM). A Primordium with ascogenous hyphae and developing paraphyses. B Later stage showing the formative layer (fl). C Section of thallus with two apothecia in different stages of development separated by a combined elevated compound margin (cm) and part of a large pycnidium (arrow). D Mature apothecium, delimited by an irregular cupular, pigmented formative layer (arrows). Scale = 50 μm.

structure. Proper margin compound, united with the thalline margin in part, thalline margin not always clearly apparent, if present, of secondary origin.

Pycnidia large, wall ± convoluted, conidiophores short-celled, conidiogenous cells producing the rod-shaped conidia terminally and laterally.

No lichen substances detected by t.l.c.

Four species are known with certainty, of which one is divided into two subspecies. One other species recorded in the literature (Zahlbruckner, 1906) may also be distinct.

Ecology and distribution: Subantarctic islands (Auckland Islands, Kerguelen Island), possibly circumpolar; also subalpine in the mountains of New Zealand. Saxicolous, terricolous, and muscicolous, often near freshwater or in areas with a high incidence of mist.

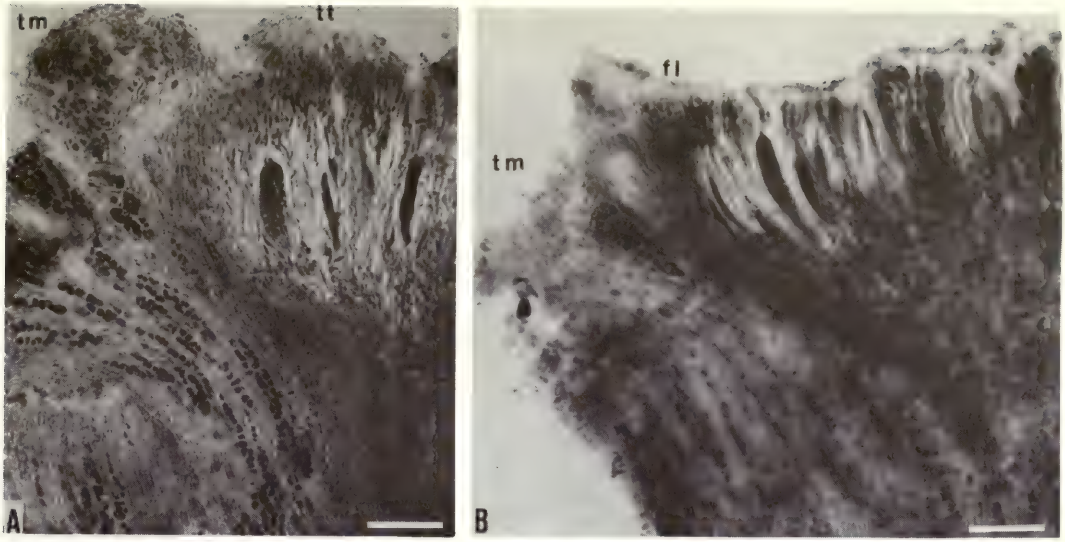

Fig. 8 *Steinera sorediata* (holotype, BM), marginal part of apothecia. A Young apothecium with secondarily developed, sorediate thalline margin (tm), the hymenium covered by remnants of thalline tissue (tt). B Old apothecium showing eroded sorediate thalline margin (tm) and adjacent pigmented formative layer. Scale = 50 μm.

Type of the genus: *Steinera glaucella* (Tuck.) Dodge.
The genus belongs to the family Coccocarpiaceae.

4. Thallus

The four species of *Steinera* are characterized by an effigurate, placoid thallus. The lobes are radiate at the margin and become more or less areolate at the centre. A notable feature of all the species is the deep and distinctive fissuring of the entire thallus. The thalli are anchored to the substrate by dark, simple or sparingly branched, rhizoidal hyphae. These structures are more apparent in *S. polymorpha* and *S. sorediata*, both species which are more loosely attached, than in *S. glaucella* and *S. radiata* which are intimately associated with the substrate.

Soralia are only present in one species, *Steinera sorediata*. The soredia are rather coarse and continuously replenished by the upward proliferation of the underlying hyphae and algal filaments. Isidia have not been observed in any species of the genus.

The anatomy of the thallus of the four species of *Steinera* follows a rather basic, uniform pattern, corresponding to the structure of other placoid lichens with blue–green phycobionts as, for example, in species of *Pterygiopsis* and *Porocyphus* (Henssen, 1963, 1974, 1979). The hyphae in the lowest part of the inner areoles are vertically orientated, but in the radiating marginal lobes the hyphae are more or less horizontally aligned, radiating fan-like along the longitudinal axis of the lobes towards the tips (Figs 12, 17, 19, 21, 23). The hyphal cells in the lower part of the thallus are elongate and thick-walled, becoming shorter, ± isodiametric, and thin-walled in the upper part. A distinct pseudoparenchymatic upper cortex is present in *Steinera radiata* (Fig. 23A–B), while in the other species the delimitation is more irregular. In all species a necrotic layer forms at the surface; this layer and part of the thallus below may become cracked, resulting in the scabrose appearance which is particularly pronounced in *S. glaucella* and *S. sorediata* (Figs 16B–D, 20A, C).

The phycobionts in the genus are *Nostoc* in *Steinera glaucella, S. polymorpha* and *S. sorediata*; a member of the Rivulariaceae occurs in *S. radiata*. In all species the algal filaments may occur in any part of the thallus except immediately below the upper surface. In those species containing *Nostoc* the algal filaments are concentrated into compact fascicles or clusters between the

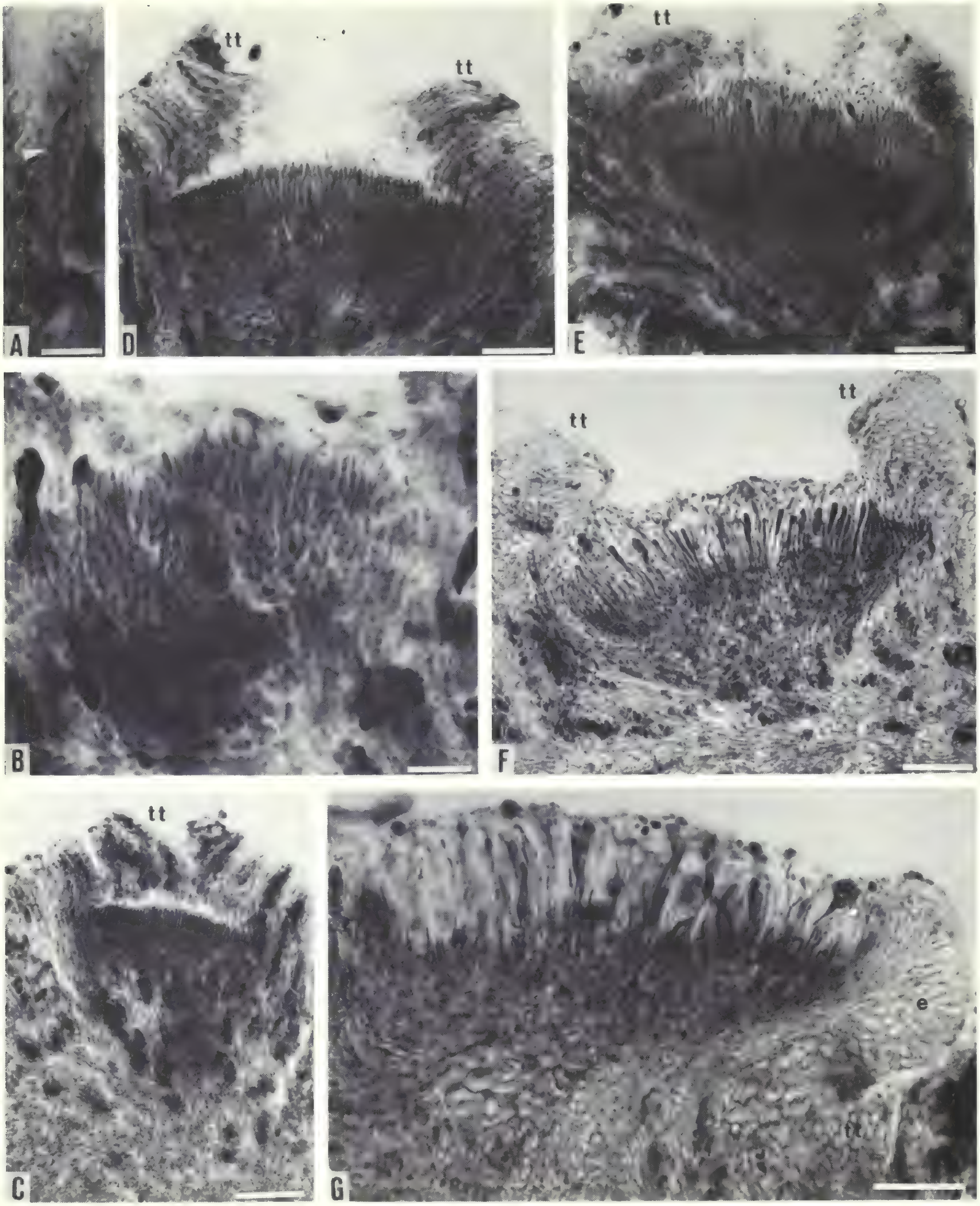

Fig. 9 Hemiangiocarpic development of the ascocarp in *Steinera radiata* subsp. *aucklandica* (holotype BM). A Coiled ascogonium with long trichogyne (arrow). B Primordium with ascogenous hyphae and developing paraphyses. C–E Young apothecia in different stages of development showing the rupture of the thalline tissue (tt) covering the hymenium. F Young apothecium, the hymenium overarched by remnants of the thalline tissue (tt). G Marginal part of very old apothecium showing a well developed excipulum proprium (e) adjacent to remnants of the thalline tissue (tt). Scale A, B = 20 μm, C–G = 50 μm.

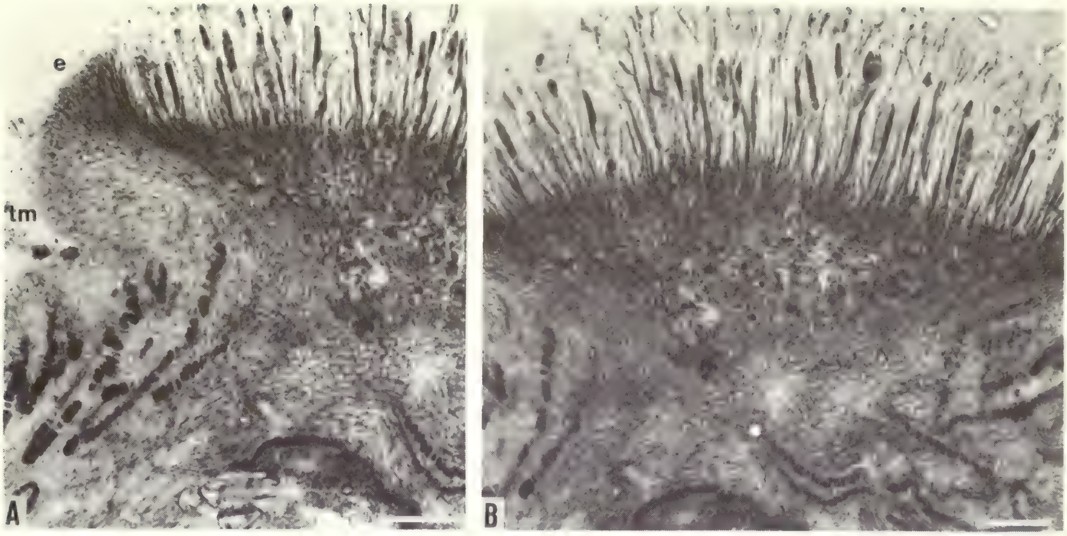

Fig. 10 *Steinera radiata* subsp. *radiata* (holotype, BM), sections of a mature apothecium. A Marginal part showing compound proper margin composed of excipulum proprium (e) and adjacent fused thalline margin (tm), thalline hyphae below subhymenium in the process of supplementing short cells to the formative layer. B Median part with lens-shaped subhymenium. Scale = 50 μm.

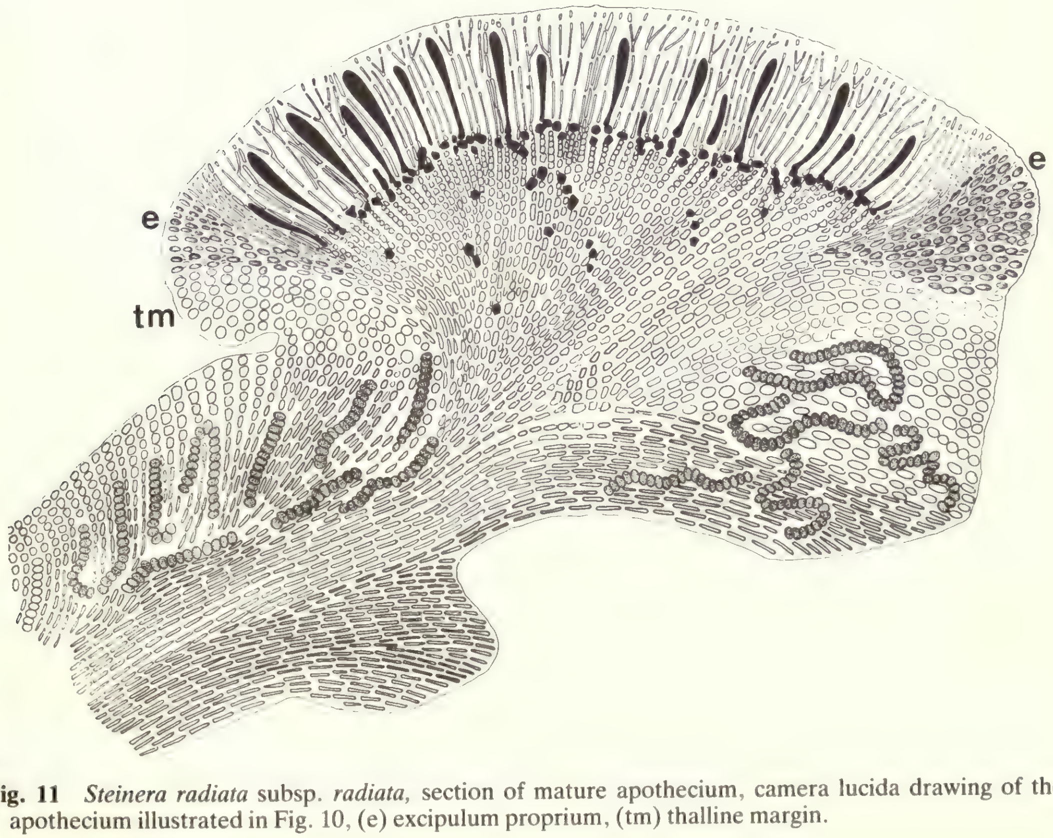

Fig. 11 *Steinera radiata* subsp. *radiata,* section of mature apothecium, camera lucida drawing of the apothecium illustrated in Fig. 10, (e) excipulum proprium, (tm) thalline margin.

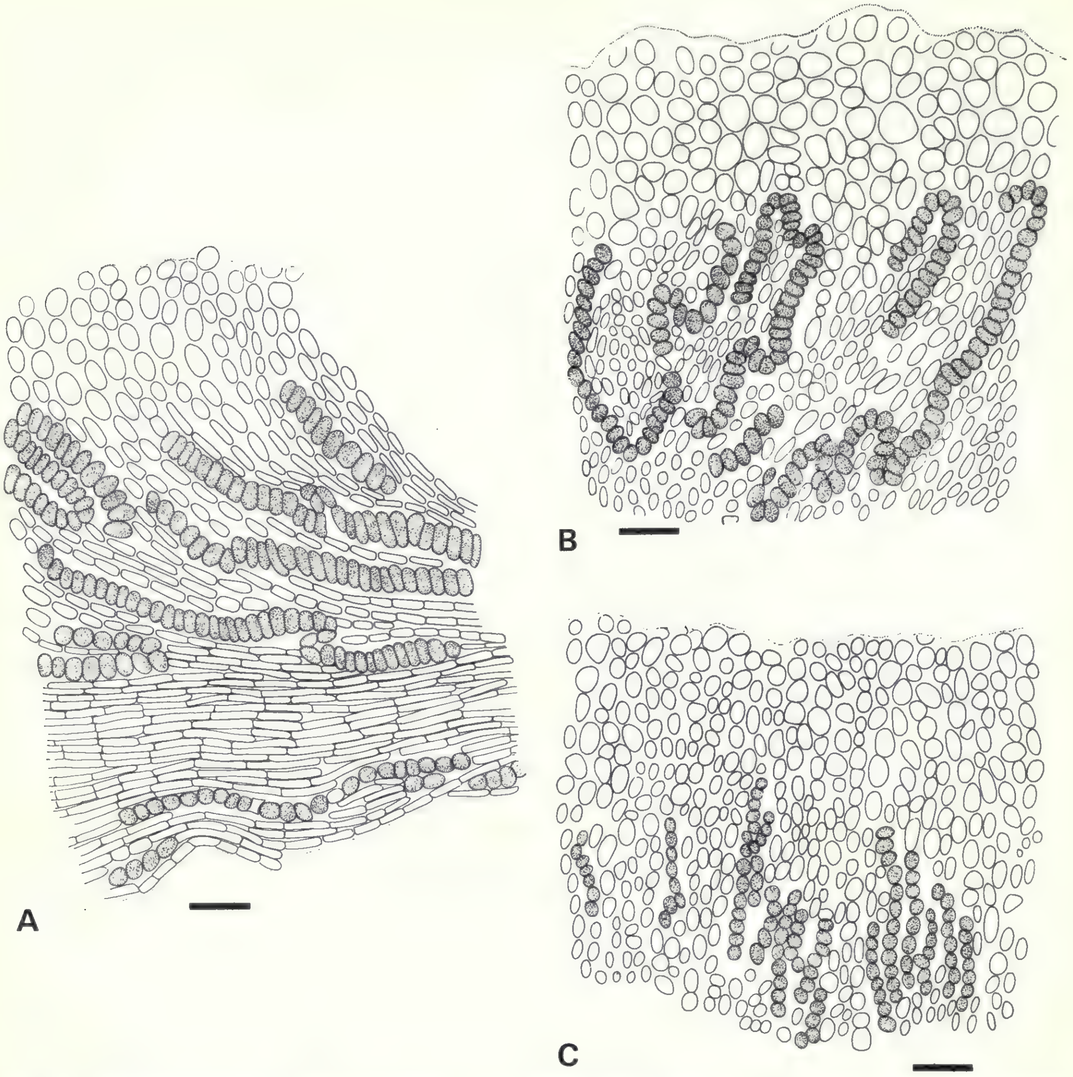

Fig. 12 Thallus anatomy of *Steinera* species. A *S. radiata* subsp. *radiata,* B *S. radiata* subsp. *aucklandica*, phycobiont a member of the Rivulariaceae, note pseudoparenchymatous upper cortex. C *S. polymorpha,* phycobiont *Nostoc*, pseudoparenchymatous cortex less well developed. Scale = 20 μm.

strands of hyphae in a broad algal zone in the upper part of the thallus (Figs 17B, 19C, 21A–B). The filaments of the phycobiont of *S. radiata* are more evenly distributed throughout the thallus. They are discrete, often convoluted and sometimes folded back (Fig. 23A–B). In this species haustoria are rather frequent, often associated with moribund or dead algal cells.

5. Fructifications

Apothecia

Apothecia are abundant in *Steinera polymorpha, S. radiata,* less so in *S. glaucella,* and rare in the sorediate species, *S. sorediata*. In *S. polymorpha* the apothecia are aspicilioid, sunken in the thallus, and have no, or a barely discernible, thalline margin (Fig. 18B–C). In *S. glaucella* the apothecia are also deeply set in the thallus; in this species a coarsely scabrid, more or less elevated thalline margin is developed (Fig. 16C). The apothecia of *S. sorediata* and *S. radiata* are emergent. In the former the thalline margin is sorediate and eroded (Fig. 20B); in *S. radiata* it is smooth and variable in colour (Figs 11, 22, 24).

The amyloid reaction of the ascus is not uniform in the genus. A ring structure is seen in the thickened apex of the ascus of *Steinera glaucella* and an amyloid cap in the three other species. This variation is similar to that which occurs in species of *Coccocarpia* (Keuck, 1977).

The spores of *Steinera radiata* are simple (Fig. 13D–E) as in *Coccocarpia, Peltularia,* and *Spilonema,* the other genera of the Coccocarpiaceae. In *Steinera glaucella* the spores are three-septate, ellipsoid with rounded ends (Fig. 13A), whereas those in *S. sorediata* and *S. polymorpha* are elongate, fusiform, multiseptate, and ± acicular at one or both ends (Fig. 13B–C).

In *Steinera glaucella* and *S. sorediata* the paraphyses are richly branched for much of their length with occasional anastomoses. In the former the apical cells are elongate and not enlarged, whereas in *S. sorediata* the upper parts of the paraphyses are somewhat enlarged and submoniliform (Fig. 13A–B). The paraphyses in *S. polymorpha* are simple below, becoming bi- or tri-furcate near the apices; the apical cells in this species are not noticeably swollen (Fig. 13C). In *S. radiata* the paraphyses are simple for much of their length and only branched near the tips. In subsp. *radiata* the apices of the paraphyses have a candelabra-like appearance but are not submoniliform, whereas in subsp. *aucklandica* the paraphyses are mostly simple and the terminal row of 3–4 cells more or less submoniliform (Fig. 13D–E). In all species the epithecium is brown; the pigmentation is external to the apices of the paraphyses.

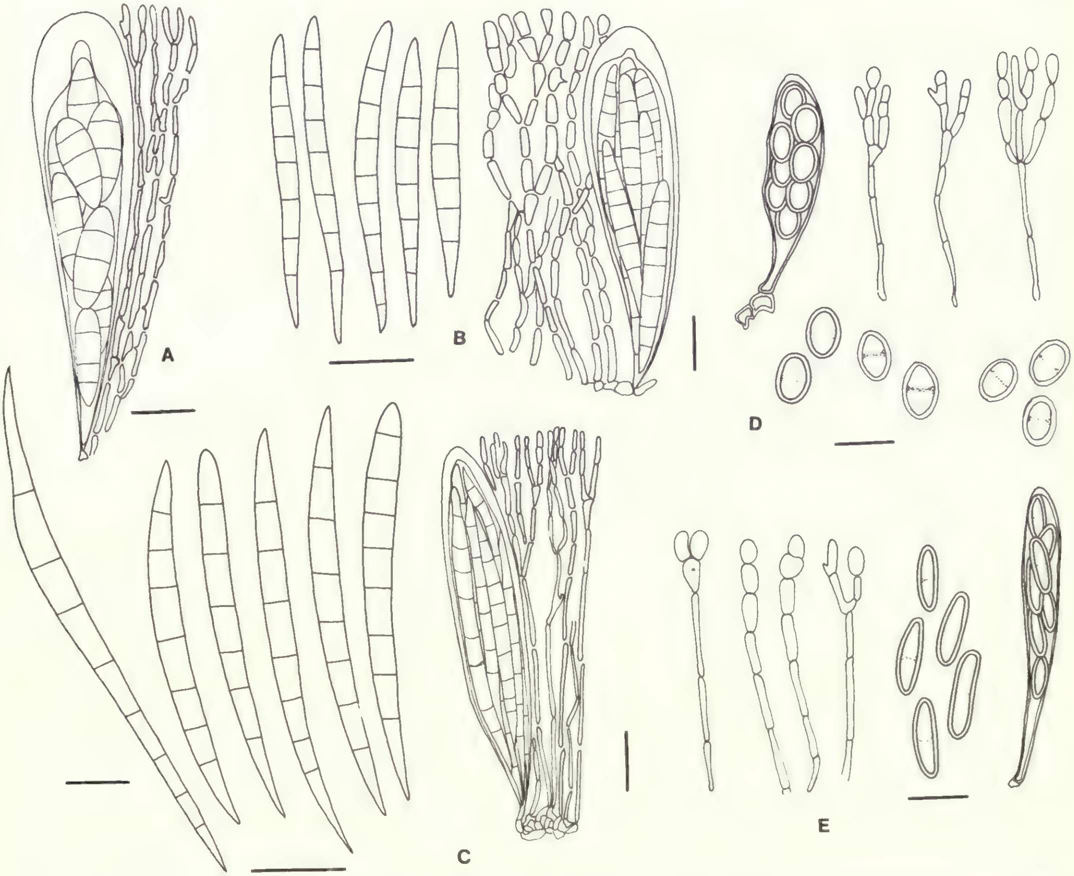

Fig. 13 Asci, spores and paraphyses in *Steinera* species. A *S. glaucella,* B *S. sorediata,* C *S. polymorpha,* D *S. radiata* subsp. *radiata,* E *S. radiata* subsp. *aucklandica.* Scale = 20 μm.

Pycnidia

Pycnidia have been observed in two species, *Steinera polymorpha* and *S. radiata*. In both species the pycnidia are relatively large, the wall is convoluted, and the conidiophores are short-celled. However, in spite of a superficial resemblance they belong to two different pycnidial types; in *S. radiata* the short conidiophores are aggregated and line the wall, leaving a relatively large, central cavity (Figs 14A, 15A–B) closely resembling the *Umbilicaria* type (Vobis, 1980: 23, Vobis & Hawksworth, 1981: 252). In *S. polymorpha* the long, richly branched-anastomosing conidiophores form a filigree arrangement which entirely fills the cavity (Figs. 14B, 15C, 19D), corresponding to the *Xanthoria* type (Vobis, 1980: 27; Vobis & Hawksworth, 1981: 254); the pycnidia of *Peltularia gyrophoroides* also belong to the same type but a central cavity is present (Fig. 15D). The conidia are shorter in *Steinera polymorpha* where they are mainly produced laterally by the conidiogenous cells (Fig. 14B); in *S. radiata* they are mainly developed terminally (Fig. 14A).

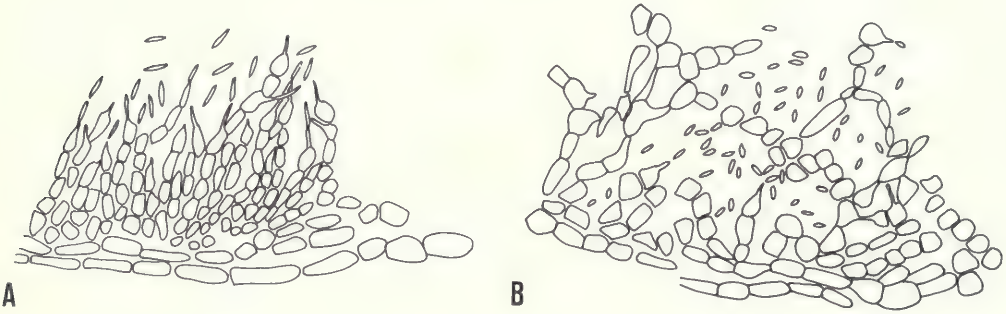

Fig. 14 Type of conidiophores in *Steinera* species. A *S. radiata* subsp. *aucklandica*, short aggregated conidiophores lining the pycnidial wall, conidiogenous cells producing conidia mainly terminally, B *S. polymorpha*, filigree network of long conidiophores, conidiogenous cells producing conidia mainly laterally.

6. Key to the species

1 Thallus copiously sorediate, rarely fertile. Apothecia with a sorediate margin. Spores elongate-fusiform, 5–7 septate, 45–57×5·5–7 µm. New Zealand .... iii. **S. sorediata** (p. 249)

– Thallus lacking soredia, usually fertile. Apothecia without a sorediate margin 2

2(1) Spores (5–) 7-septate, elongate-fusiform, 65–75×5–5·5 µm. Thallus thick, polymorphic, in part radiating, loosely attached to mosses, stones and soil. New Zealand .. ii. **S. polymorpha** (p. 246)

– Spores simple to 3-septate, ellipsoid or subglobose, not exceeding 20 µm in length. Thallus closely affixed to stones and rock, margin always radiate 3

3(2) Central areoles convex, surface more or less scabrid. Asocarps more or less innate, remaining concave, disc pale brown to brown. Spores (1–) 3-septate, ellipsoid. 19–21×6–7 µm. Kerguelen Island .... i. **S. glaucella** (p. 243)

– Central areoles plane, surface smooth. Asocarps emergent to sessile, disc dark brown. Spores simple and with a plasma bridge, less than 40 µm in length 4

4(3) Spores subglobose or shortly ellipsoid, 8–10·5×6·5–7·5 µm. Paraphyses branched at the apices, not submoniliform. New Zealand .... iv. **S. radiata** subsp. **radiata** (p. 252)

– Spores ellipsoid, 12–14×3–4·5 µm. Paraphyses simple or bifurcate at the apices, upper part submoniliform. Auckland Islands ....iv. **S. radiata** subsp. **aucklandica** (p. 253)

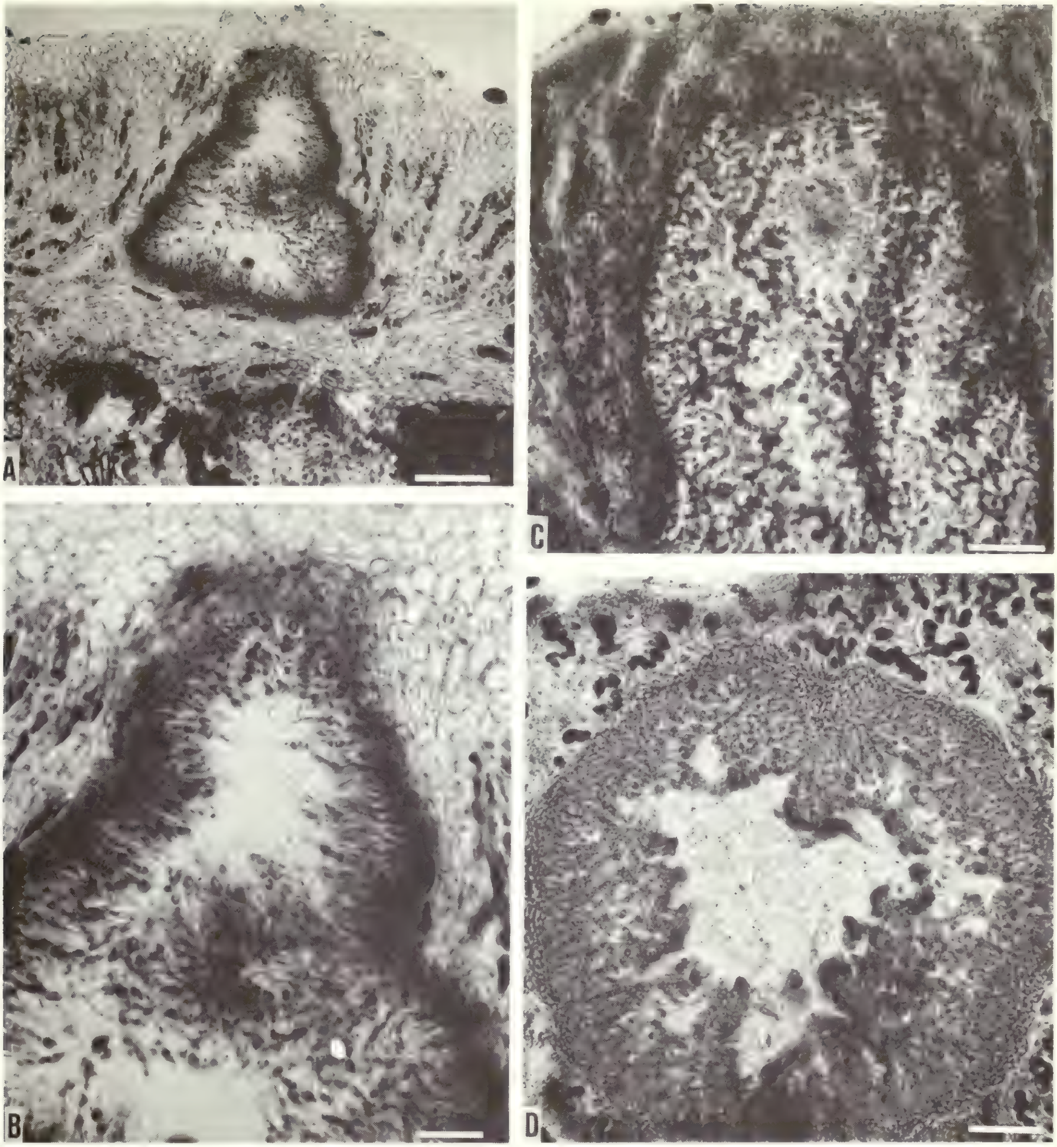

Fig. 15 Types of pycnidia in *Steinera* and *Peltularia*. A–B *S. radiata* subsp. *aucklandica* (holotype, BM); A Irregularly shaped pycnidium within algal zone, B Upper part in higher magnification showing aggregated conidiophores. C *S. polymorpha,* part of pycnidium filled with branched conidiophores. D *P. gyrophoroides,* pycnidium of same type as in *S. polymorpha*. Scale A, C, D = 50 μm; B = 20 μm.

7. The species

i. Steinera glaucella (Tuck.) Dodge in *B.A.N.Z. Antarct. Research Exped. 1929–31, Reports* B, **7**: 66 (1948).

Figs. 4A–C, 5A–E, 6A–B, 16A–C, 17A–D.

Pannaria glaucella Tuck. in *Bull. Torrey bot. Club* **6**: 57 (1875). Type: Kerguelen Island, 1875, *Kidder* (U.S. Transit Expedition) (FH—holotype).

Amphidium molybdoplacum [‘*molybdophæum*’] Nyl. ex Crombie in *J. Bot. Lond.*, **13**: 333 (1875); [‘*molybdoplacum*’] in *J. Linn. Soc.* (Bot.) **15**: 181 (1876). *Steinera molybdoplaca* (Nyl. ex Crombie)

Zahlbr. in *Deutsche Südpolar-Expedition 1901–1903* **8**: 43 (1906). Type: Kerguelen Island, Swain's Bay, December 1874, *A. E. Eaton* (Venus Transit Expedition) (BM—lectotype; BM, H—isolectotypes).

Thallus irregular or forming ± complete rosettes, to 6 cm diam., closely appressed to the substrate and not easily detached without damage, uniformly pale grey or becoming darker grey towards the centre, sometimes with an olive tinge, margins shortly radiating, ± lobate. Marginal lobes flabellate, broadening to 2 mm towards their convex ends and there occasionally notched, separated by deep intersecting fissures with dentate edges; centre of thallus with coarse, angular, predominantly convex, complete or incomplete, areoles derived from secondary rimose cracking between the main fissures; entire surface of the thallus roughened, sometimes coarsely scabrid, matt.

Ascocarps rather scarce, scattered or sometimes 2 (–4) contiguous, developed on the uppermost part of the older, inner areoles, 3–8 mm diam., deeply innate at first, eventually more or less level with the surface of the thallus, urceolate; disc dull brown to deep red–brown, smooth or slightly roughened, thalline margin not or slightly elevated, markedly scabrose, sometimes appearing spuriously sorediate.

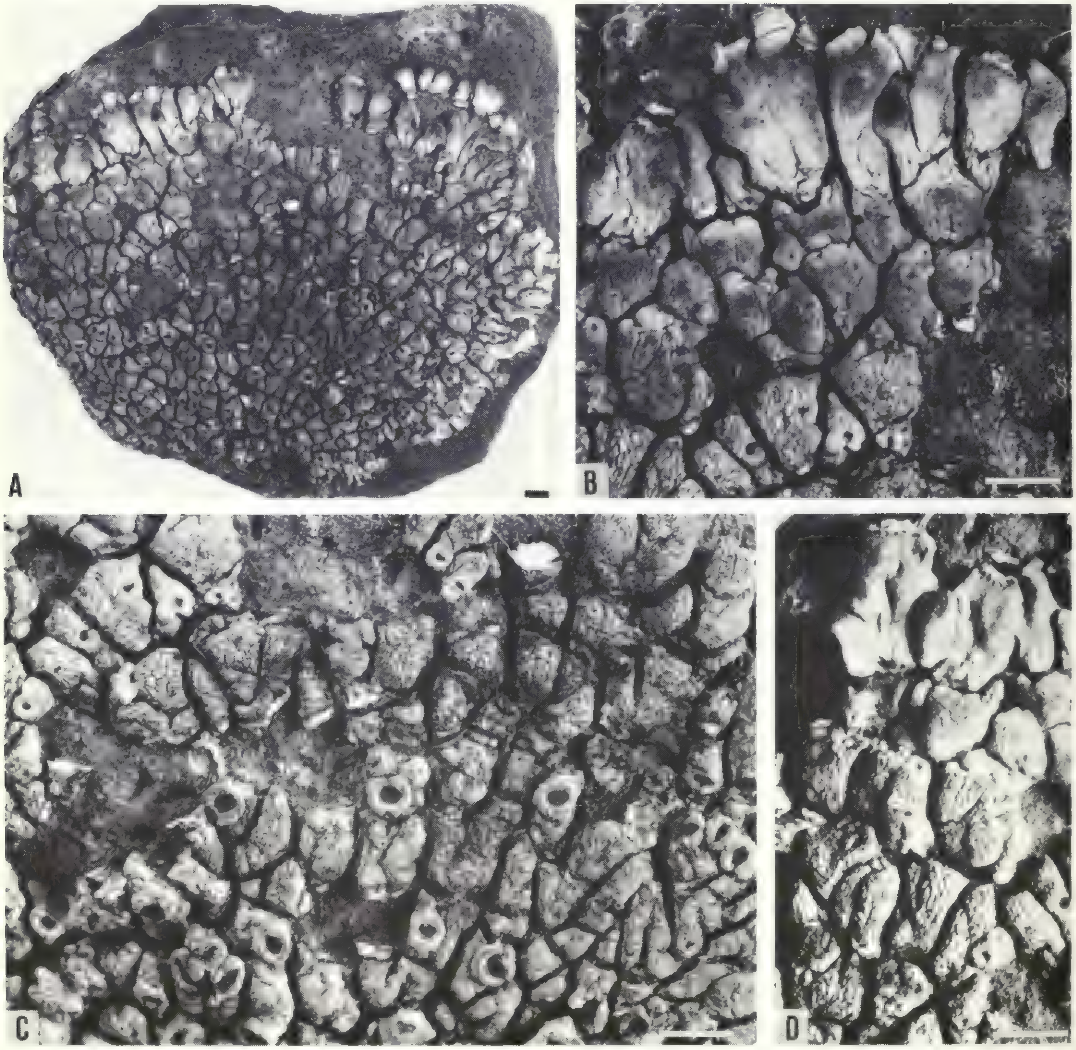

Fig. 16 A–D Habit photographs of *Steinera glaucella* (lectotype of *S. molybdoplaca*, BM). Scale = 2 mm.

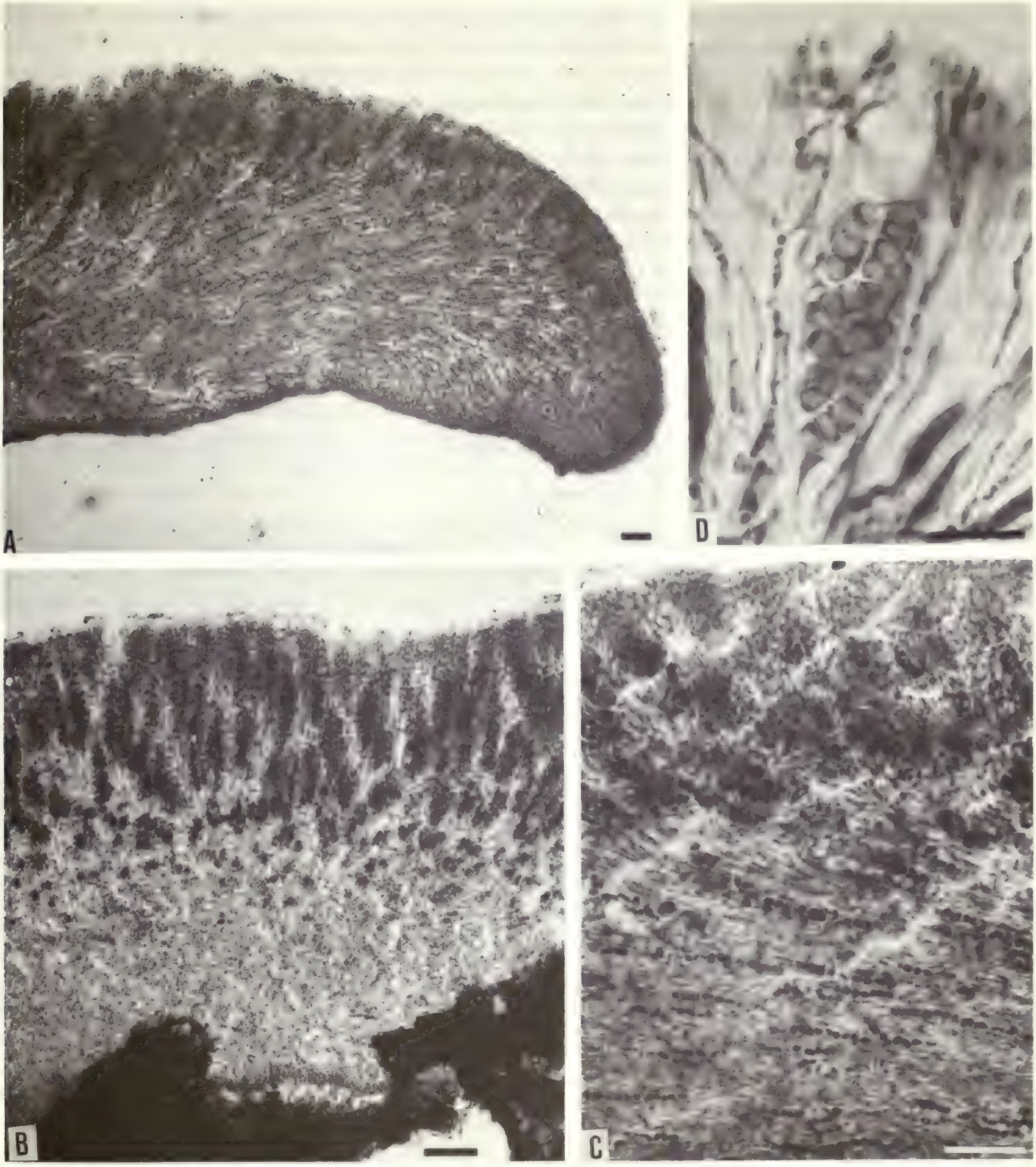

Fig. 17 Anatomy in *Steinera glaucella* (lectotype of *S. molybdoplaca*, BM). A–C Sections of thallus; A L.s. of lobe tip, B T.s. of central area, C L.s. in higher magnification. D Ascus with thickened apex (arrow) and spores. Scale A, C, D = 50 μm; B = 20 μm.

Thallus *c.* 1000 μm thick, without a distinct upper cortex but older parts of the thallus with a thin, amorphous, semi-translucent, uneven layer overlying a ± algal-free layer, 5–40 μm thick, of mostly vertically aligned, thin-walled, oval, rounded or slightly cuboidal cells, ± uniform in size, 7–10 μm. Phycobiont a species of *Nostoc,* cells 6–8 μm, mainly concentrated in a broad zone *c.* 60 μm thick, occurring in vertically orientated fascicles between the fan-shaped ascending hyphae, algal cells 15–18×5–7 μm. Below the phycobiont zone the hyphae are closely compacted, either vertically aligned as in the central areoles, or ± horizontally radiating towards the apices of the marginal lobes, generally interspersed with simple chains of algal cells. Lower part of thallus brown–black, composed of periclinal hyphae with blackened walls. Simple or rarely branched rhizoidal hyphae anchor the thallus to the substrate.

Thecium 150–180 μm, epithecium more or less pale brown. Asci 120–140×13–16 μm, elongate-clavate or sometimes almost cylindrical, apices up to 10 μm thick, with an apical ring structure. Spores mainly biseriately arranged (4–7) –8 per ascus, (1–) 3-septate, ovoid, straight or slightly curved (15–) 19–21×6–7 (–9) μm, thin-walled. Paraphyses distinct, in a gelatinous matrix, richly branched with scattered interconnecting anastomoses, apical cells shortened and somewhat swollen. Excipulum-like structure (formed by formative layer) slightly pigmented, *c.* 50 μm thick, cupular, composed of small, deeply staining (in lactophenol-cotton blue), nubiliated, cuboid cells, 5–7×5–6 μm; at the outer edge, extending upwards to form the inner part of the overarching thalline margin which contains clusters of algal cells. Subhymenium lens-shaped, up to 200 μm thick, of short-celled, vertical hyphae permeated by thicker ascogenous hyphal filaments.

Pycnidia not observed.

Specimens seen:
Kerguelen: *Kidder* (holotype of *Pannaria glaucella*); Swain's Bay, *Eaton* (type collections of *Amphidium molybdoplaca*).

Observations:
Steinera glaucella is distinguished by the rosette-shaped, closely appressed thallus with convex central areoles and more or less radiating marginal lobes (Fig. 16A–B), the urceolate ascocarps with only slightly elevated, scabrid thalline margins (Fig. 16C), and the short, three-septate spores (Figs 13A, 17D).

Pannaria glaucella Tuck. was published one month earlier (October 1875) than *Amphiloma molybdoplaca* Nyl. ex Crombie (November 1875), a fact to which Tuckermann drew attention in a subsequent paper (1877). The holotype on which Tuckermann's description of *Pannaria glaucella* is based is a small specimen, barely 1 cm in diameter, with immature apothecia. Although this specimen has been badly damaged by mites and abrasion, the few lobes which remain intact have the characteristic roughness to scabrid surface and internal anatomy, including 'Collogonidia 0·004–9 mm in diameter, in chains often 4–10', found in the abundant type material of *Steinera molybdoplaca* (Nyl. ex Crombie) Zahlbr. The two gatherings are therefore considered to represent the same species, the name *S. glaucella* taking priority as indicated by Dodge (1948).

Even if *Steinera glaucella* and *S. molybdoplaca* had been found to be different entities the specific epithet *molybdoplaca* was rendered nomenclaturally superfluous when published (Art. 63). This is because the earlier name *Pannaria glaucella*, which should have formed the basionym, is cited in the synonymy of Zahlbruckner's new combination *Steinera molybdoplaca*, which was based on *Amphidium molybdophaeum* which was published a month later. With regard to the difference in spelling, Crombie (1876, loc. cit.) remarks: 'This was erroneously printed as *molybdophæum* in "Journ. Bot."'.

ii. **Steinera polymorpha** P. James & Henssen, **sp. nov.**

Figs 7A–D, 12C, 13C, 14B, 15C, 18A–C, 19A–D.

Thallus supra solum, muscos lapidesque, plus minusve placodioideus, laxe affixus, ad 5 cm diam., polymorphus, pallide cremeus vel caesiellus, marginibus plus minusve lobatis, crustaceus areolatusque in centro fissus, sorediis nullis praesentibus. Alga ad genus *Nostoc* pertinens. Apothecia crebra, 0·4–0·9 mm diam., 3–4 saepe confluentia, innata, urceolata, marginibus inconspicuis; discus obscure rufescenti-fuscus, concavus semper. Hymenium usque ad 150 μm; asci 100–110×16–25 μm, apice incrassato et amyloideo. Sporae (5–) 7-septatae, elongato-fusiformes, (55–) 65–75×(4·5–) 5–5·5 (–6·5) μm. Pycnidia numerosa, in sectione ad 0·08 mm lata; conidia praecipue terminaliter formata, bacilliformia, 4–5×1·5 μm, conidiophoris longis, articulatis et anastamosantibus.

Typus: New Zealand: South Island, Fiordland, Dusky Sound. In iugo super Cascade Cove, 1000–1200 m, supra solum et lapides muscis vestitos in pratis subalpinis, 10 February 1967, *D. J. Galloway* (BM—holotypus; CHR—isotypus).

Thallus ± placoid, spreading, to 5 cm diam., polymorphic, overgrowing rocks, bryophytes and soil, rather loosely attached to the substrate, margin lobate; marginal lobes radiating, ± distinct up to 2 mm wide, contiguous, rarely overlapping, apices rounded, sometimes notched, flabellate. Upper surface often coarsely scabrose, pale cream to pale blue–grey, older parts conspicuously radially fissured, areolate with numerous, anastomosing, coarse ridges and fissures.

Apothecia 0·4–0·9 mm diam. when mature, at first urceolate, deeply immersed in the thallus, gradually emergent, thalline margin at first inflexed, later not apparent or only slightly elevated above the disc. Apothecia discrete at first, later becoming 2–4-confluent, sometimes the combined discs dissected by fine to rather coarse fissures; discs dark red–brown, slightly roughened, often shining.

Pycnidia numerous, seen as small, rather irregular, dark brown spots on the surface of both young and old areas of the thallus, not easily distinguishable from apothecial primordia without microscopic examination.

Thallus *c.* 1000 μm thick, upper algal-free zone very irregular in thickness, 70–150 μm thick, composed of thin-walled, isodiametric or slightly elongate, closely compacted cells in the upper part, forming a ± pseudoparenchymetous layer, of enlarged cells, 7–11·5×7–13·5 μm, overlaid by a semi-transparent, uneven surface layer of necrotic cells. Phycobiont a species of *Nostoc,* mainly concentrated in a zone *c.* 500 μm thick, individual cells, 4·5–6 μm. Filaments crowded into elongate, vertically orientated fascicles between the fan-like ascending hyphae, hyphal cells 15–23×4·5–5·5 μm. Hyphae at thallus base elongate, closely contiguous and ± horizontally

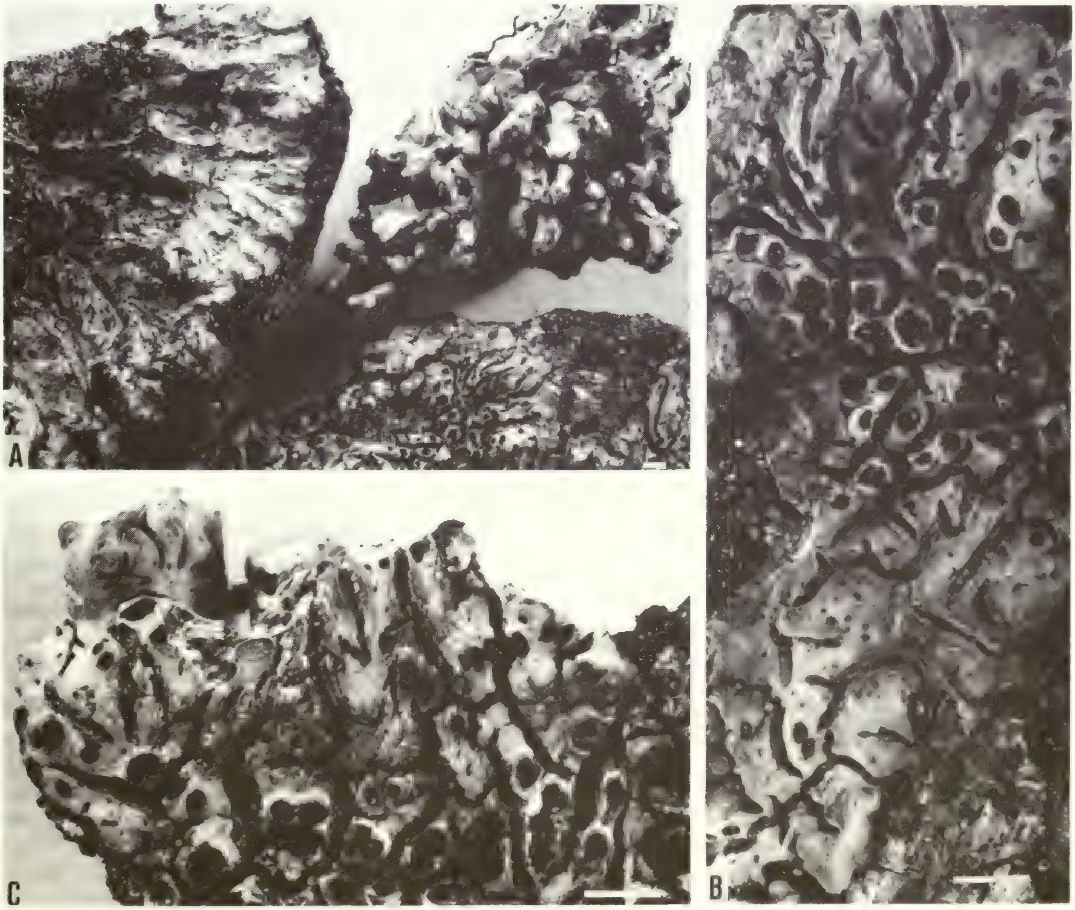

Fig. 18 Habit photographs of *Steinera polymorpha* (holotype, BM). Scale = 2 mm.

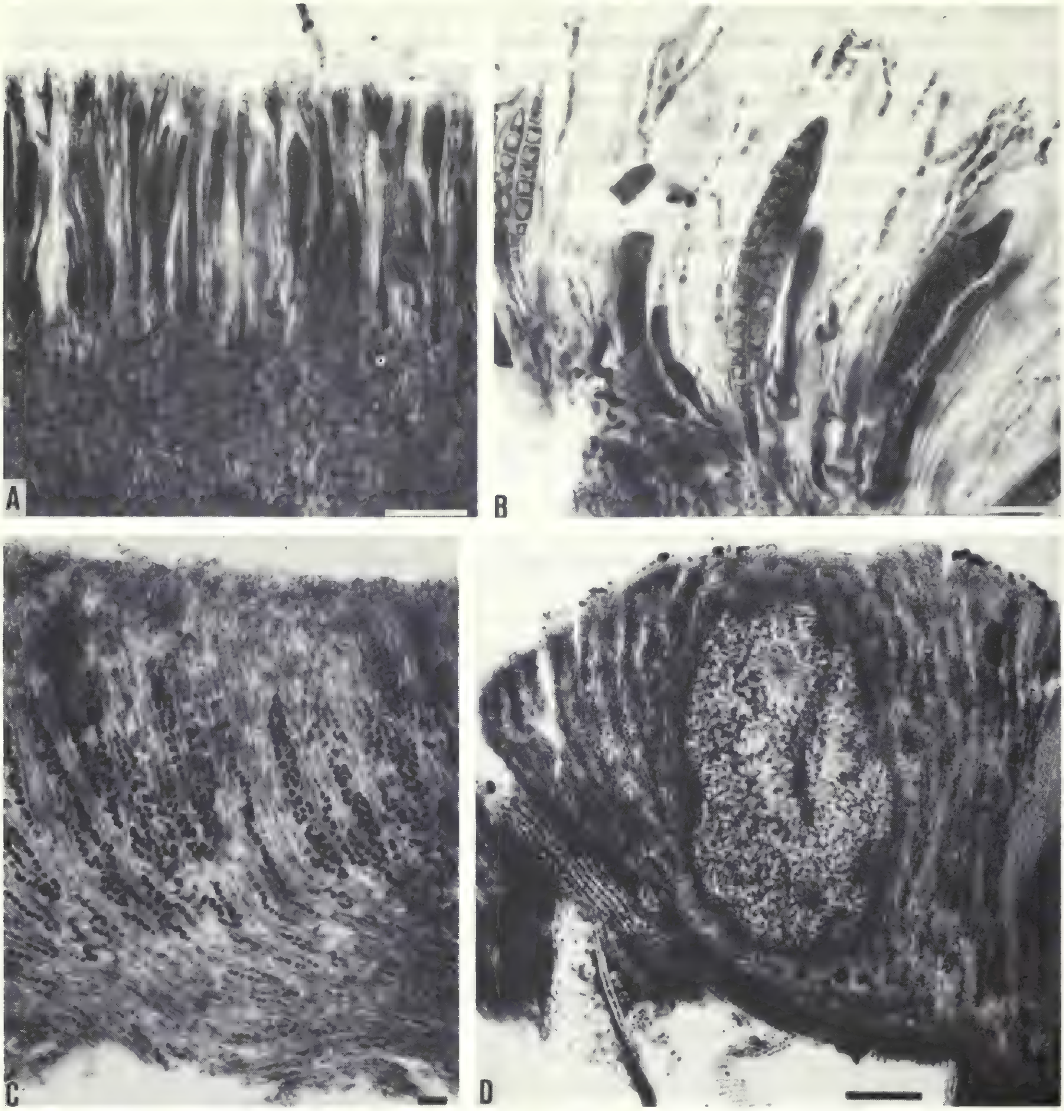

Fig. 19 Anatomy in *Steinera polymorpha* (holotype, BM). A part of hymenium. B Asci and paraphyses. C L.s. of thallus. D Thallus section with large pycnidium. Scale A, C, D = 50 μm; B = 20 μm.

aligned ascending towards the centre of the thallus or horizontally spreading into the marginal parts of the lobes by scattered single algal filaments. Lower surface ± brown–black developing dark-walled, rhizoidal, simple hyphae which penetrate the substratum.

Thecium *c.* 150 high, epithecium pale brown, semi-opaque. Asci 100–110×16–25 μm, clavate or elongate-clavate, widening towards the apex, apices of ripe asci thickened to up to 5 μm, an amyloid cap but no ring structure present. Spores elongate-fusiform, with one or both ends more or less tapered, (55–) 65–75×(4·5-) 5–5·5 (–6·5) μm, (5–) 7-septate, spore cells equal in length. Paraphyses conspicuous in a gelatinous matrix, simple below, often furcately branched towards the apices, cells of lower part *c.* 1·7 μm wide, to 2·5 μm towards the apices, terminal cells sometimes collapsed and necrotic. Exciple-like structure of the formative layer pigmented, cupuliform, *c.* 50 μm thick, composed of small, closely compacted cells with deeply staining contents (in lactophenol-cotton blue), incorporated at the overarching inner edge of the thalline margin in young apothecia; thalline margin not distinct in older ascocarps. Subhymenium up to

150 μm high, of closely compacted, short-celled hyphae which include more or less vertically aligned ascogenous hyphae in the upper part.

Pycnidia of *Xanthoria* type (see p. 242), in section large, globose to ellipsoid, up to 600 μm broad and 800 μm wide; conidiophores repeatedly branched to form a filigree-like network inside the pycnidium (Figs. 15C, 19D); conidiogenous cells mainly producing conidia laterally; conidia 4–5×1·5 μm, ellipsoid to slightly rod-shaped (Fig. 14B).

Specimen seen:
New Zealand: South Island, Fiordland, Dusky Sound, Cascade Cove, *D. J. Galloway* (type collection).

Observations:
As indicated by the choice of specific epithet, *Steinera polymorpha* has a very variable morphology (Fig. 18A–C). Although the centre of the thallus may be considerably contorted, convoluted, and ridged, the marginal lobes and effigurate shape are characteristic for the genus. The entire thallus is deeply and widely fissured.

The new species can be easily distinguished from other taxa in the genus by the aggregated aspicilioid apothecia and the relatively long spores. *S. polymorpha* is closely related to *S. sorediata*, which has similar but shorter spores tapering at one or both ends; further differences are the abundantly sorediate thallus, and the formation of a distinct thalline margin around the apothecia.

The new species was collected from *Chionochloa*-dominated subalpine grassland on an exposed west-facing ridge above Cascade Cove. The climate in the region is severe with a high rainfall (up to 90 cm per annum) and often long periods of mist. It occurs on poorly drained, podsolized soil associated with the moss *Andreaea rupestris* and the lichens *Siphula complanata, S. fragilis,* and *Placopsis* spp.; in nearby grassland *Cladia inflata* and *Menegazzia inflata* are more or less frequent.

iii. Steinera sorediata P. James & Henssen, sp. nov.
Figs. 8A–B, 13B, 20A–D, 21A–D.

Thallus supra rupes, per solum et bryophyta extendens, usque ad 6 cm diam., irregulatim placodioideus, plus minusve laxe affixus, substramineus vel pallide lilacino griseus, marginibus plus minusve lobatis, crustaceus areolatusque in centro fissus, sorediatus. Soralia numerosa, saepe confluentia, dilute caesia vel lilacina. Alga ad genus *Nostoc* pertinens. Apothecia rara, 0·4–0·7 mm diam., innata, plus minusve emergescentia, margine paulo elevato, saepe fere ubique sorediato; discus rufo-badius vel brunneus, paulo concavus vel planus. Hymenium ad 220 μm; asci 160–170×12–14 μm, apice incrassato et amyloideo. Sporae (3–) 5–7-septatae, aciculari-fusiformes, (37–) 45– (–75)×(5–) 5·5–7 (–8) μm. Pycnidia non visa.

Typus: New Zealand: South Island, Otago, Dunedin, Mount Cargill. Prope verticem ad rupes plus minusve nudas, cum *Menegazzia circumsorediata,* 9 January 1963, *P. W. James* NZ 2099/2 (BM—holotypus; BM, CHR, MB, US—isotypi).

Thallus predominantly placoid, spreading, to 6 cm diam., overgrowing rock, soil, and bryophytes, rather loosely attached to the substrate, pale stramineous, pale mauve–grey, or pale grey, margin conspicuously lobate. Lobes radiating, apices and margins slightly raised, contiguous except near their ends, ± flabellate towards the tips, 1·5–2·5 mm wide, often overlapping, radially fissured, surface becoming conspicuously and irregularly radially undulate and corrugate, in places folded, often with radial and some transverse anastomosing fissures and radiating ridges. Surface markedly scabrose-roughened, especially towards the tips of the lobes. Central part of the thallus subcrustose, ± continuous with deep, partially interconnected fissures. Soralia laminal, numerous, originating especially from a breakdown of ridges, rounded or more frequently oval or elongate, becoming irregular and more or less confluent, in some specimens soredia ± covering the entire upper surface of the thallus. Soralia efflorescent, pale blue–grey or lilac, coarsely granular, occasionally with a few finger-like, coralloid isidia which become partly dissolved in soredia.

Apothecia rather rare, widely scattered, 0·4–0·7 mm diam., at first innate, gradually more or less emergent with a slightly elevated thalline margin when mature; disc bright red–brown to

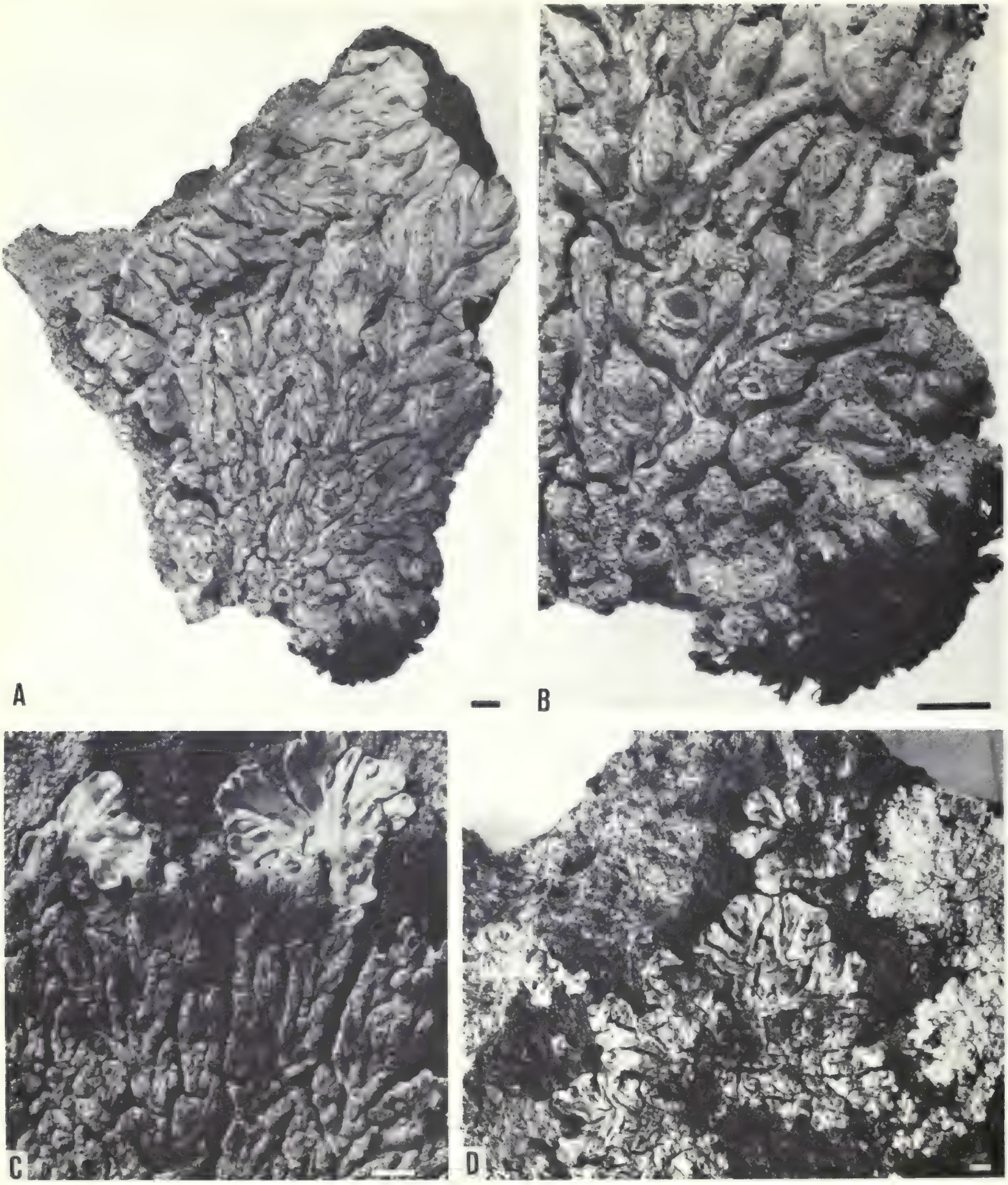

Fig. 20 A–D Habit photographs of *Steinera sorediata*. Scale = 2 mm.

brown, smooth or slightly roughened, slightly concave or plane, margin rather thin, 0·5 mm wide, in part smooth, mostly or entirely granular sorediate.

Thallus *c.* 400 μm thick, with an upper, algal-free zone, *c.* 50 μm high, composed of ± anticlinally organized, ± isodiametric cells, 8–12×5–9 μm, thin-walled and colourless, becoming collapsed and moribund at the surface to form a very thin, hyaline surface layer. Phycobiont a species of *Nostoc*, violet–blue, cells 3·5–7 μm, filaments concentrated in a zone 200–250 μm high in elongate, ± vertically orientated clusters between anticlinal strands of hyphae, hyphal cells thin-walled, 14–20×4·5–5 μm. Lowest thallus zone *c.* 150 μm, mainly composed of horizontally aligned, rather compacted, thick-walled hyphae. Scattered, single chains of *Nostoc*

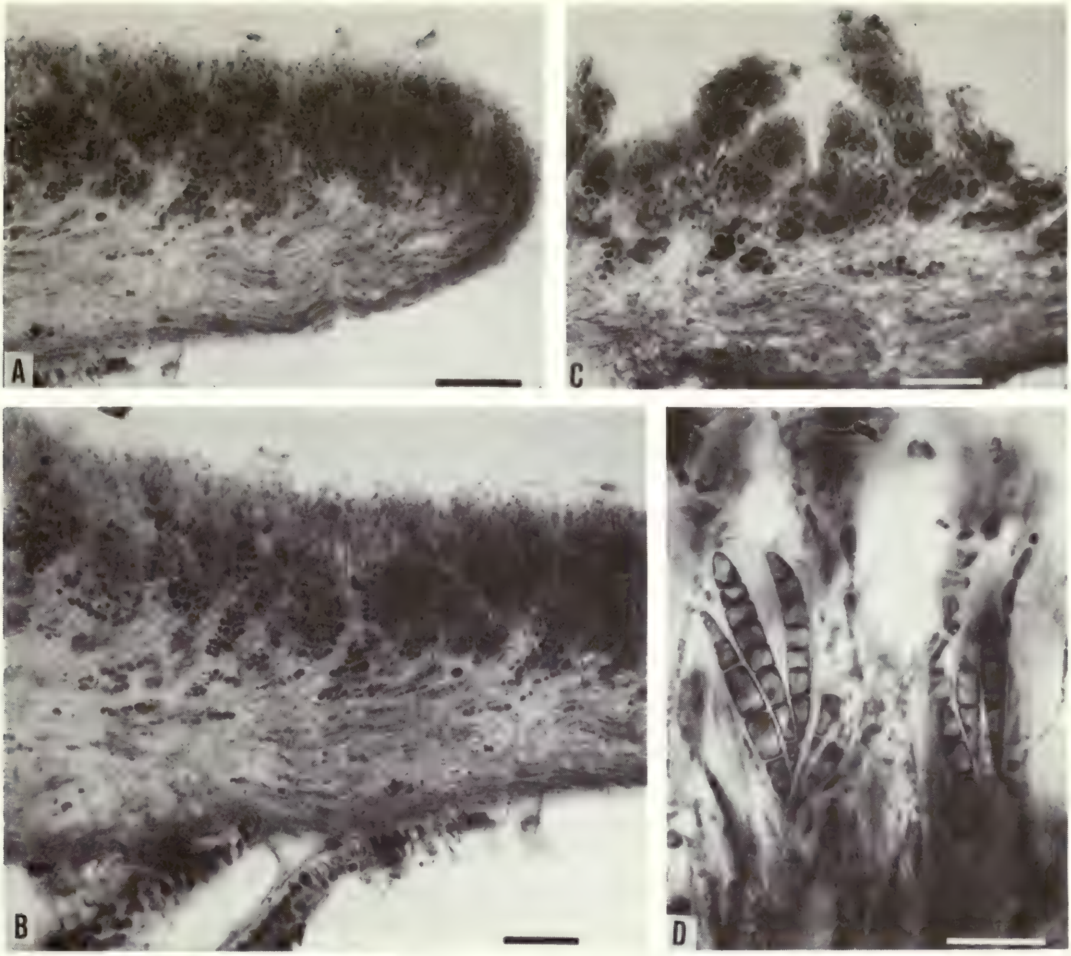

Fig. 21 Anatomy in *Steinera sorediata* (holotype, BM). A L.s. of lobe tip. B L.s. of older part. C Development of soredia. D Squash preparation of asci and paraphyses, note the multi-septate spores. Scale A, B, D = 50 μm; C = 20 μm.

also occur between these hyphae. The hyphae in proximity with the substrate have dark brown walls and tend to elongate into rhizoidal extensions into the substrate.

Soredia up to 60 μm, often between 30–50 μm diam., composed of extruded, irregular or rounded clusters of algal cells surrounded by a compact envelope of hyphae with thin-walled, cuboidal or rounded cells.

Thecium *c.* 200 μm high, epithecium more or less red–brown, colour contained in the gelatinous matrix surrounding the tips of the paraphyses. Asci 160–170×12–14 μm, clavate, broadening toward the apex, apex up to 5 μm thick. Spores 8 per ascus, bunched, (37–) 45–57 (–75)×(5–) 5·5–7 (–8) μm, (3–) 5–7-septate, acicular—fusiform with one or both ends tapered. Paraphyses distinct in a gelatinous matrix, simple at their base, becoming furcately branched and sparingly anastomosing above, cells rather short, sub-moniliform, enlarged to *c.* 5 μ at apex. Annular exciple-like structure of the formative layer, poorly developed, *c.* 45 μm thick, composed of very small, deeply staining periclinally arranged hyphae with cuboidal cells, 3–4 μm in size. Subhymenium up to 300 μm thick, of unorientated anticlinally arranged hyphae with short cells and vertically aligned ascogenous hyphae in the upper part adjacent to the thecium. Thalline margin similar in structure to the sorediate part of the thallus, the cortex dissolved in characteristic soredial clusters.

Pycnidia not observed.

Specimens seen:
New Zealand: North Island, Mount Egmont, Tahurangi Bluff, *J. K. Bartlett*, 14 December 1977 (BM, CHR). South Island, Otago, Dunedin, Mount Cargill, fertile, *P. W. James* NZ 2099/2 (type collection); Otago, Dunedin, on mossy rocks near the summit of Flagstaff Hill, 580 m, sterile, December 1958, *J. Murray* 3696 (BM, OTA); Otago, Dunedin, Mount Cargill, near summit in sheltered, rather damp, mossy clefts, 640 m, sterile, January 1959, *J. Murray* 3791 (BM, OTA); Otago, Dunedin, Mount Cargill, with *Placopsis parellina,* 670 m, sterile, January 1959, *J. Murray* 3793 (BM, OTA).

Observations:
Steinera sorediata is distinguished from all other species of the genus by the presence of soralia. These are abundantly produced in all specimens seen and often cover extensive areas of older parts of the thalli (Fig. 20B–C). In outward appearance *S. sorediata* might superficially be mistaken for a species of *Physconia*, but the presence of *Nostoc* as the phycobiont in the former distinguishes it immediately. The habit of *Steinera sorediata* is also reminiscent of the cyanophilic species *Vestergrenopsis isidiata,* although this species is smaller in size and has isidia.

The presence of multiseptate, ± acicular spores suggests that *Steinera sorediata* may be closely related to *S. polymorpha.* Even so, there are some differences in their ontogeny and anatomy which suggest that they cannot be considered as a species pair.

Variation in the species is confined to the size, distribution, and organization of the marginal lobes and the degree of soredial development.

Steinera sorediata is a saxicolous species on rock outcrops in subalpine grassland with *Hebe elliptica, Dracophyllum longifolium, Phormium tenax,* and *Aciphylla* spp. Associated lichens are *Placopsis parellina, P. perrugosa, P. cribellans, P. gelida, Parmelia signifera,* and *Menegazzia circumsorediata.*

iv. **Steinera radiata** P. James & Henssen, **sp. nov.**
subsp. **radiata**
Figs 10A–B, 11, 12A, 13D, 22, 23A, F.

Thallus saxicolus, placodioideus, perfecte rosulatus, ad 4 cm diam., pallide griseus vel caesius, arcte appressus, marginibus regulatim lobatis, radiatus in centro crustaceus, regulatim areolato-fissus, sorediis nullis praesentibus. Alga verosimiliter ad familia Rivulariacearum pertinens. Apothecia crebra, 0·5–0·9 mm diam., innata, gradatim plus minusve sessilia; discus planus vel convexus, obscure vel laete rufo-badius, margine thallino coloribus variis, pallide griseo vel rufo-badio. Hymenium ad 60 μm; asci 50–55×10–15 μm, apice incrassato et amyloideo. Sporae curte ellipsoideae vel plus minusve globosae, eseptatae, ponticulo e plasmate mediano, (7·5) 8–10·5×(5·5) 6·5–7·5 μm. Paraphyses cellula apicali ad 7 μm aucta.

Typus: New Zealand: South Island, Fiordland Botanical District, Mount Barber. Supra saxa in amne, in asperis subalpinis super Deep Cove, 3 March 1927, *G. Einar & Greta Du Rietz* 2063: 1 (BM—holotypus; CHR, MB, UPS (Du Rietz)—isotypi).

Thallus to 4 cm diam., rosette-shaped, very closely appressed, not detachable from the substrate without damage, placoid, radiate, markedly effigurate, the centre becoming areolate—crustose, pale grey to pale blue–grey. Marginal lobes regular, contiguous for their entire length but frequently separated by deep, coarse, radiating fissures, lobe ends slightly flabellate, 0·25–0·5 mm wide, 3–4 mm in length; central areoles derived from rimose cracking, 0·5–0·9 mm diam., irregular with angular margins, fissuring particularly distinct when dry. Surface overall plane or slightly uneven, matt, sometimes slightly scabrose on the marginal lobes.

Apothecia frequent, mostly restricted to the central, crustose area of the thallus, 0·5–0·9 mm diam., at first innate, hemiangiocarpic, slowly becoming emergent when mature, eventually appearing superficial and adnate on the thallus surface, rounded or slightly elliptical, discrete, rarely confluent; disc dull to bright red–brown, convex from the first, remaining so when mature or becoming plane, surface finely roughened. Young apothecia covered by rupturing thalline tissue, proper margin gradually exposed so that in old apothecia it is well developed to ± 1 mm thick.

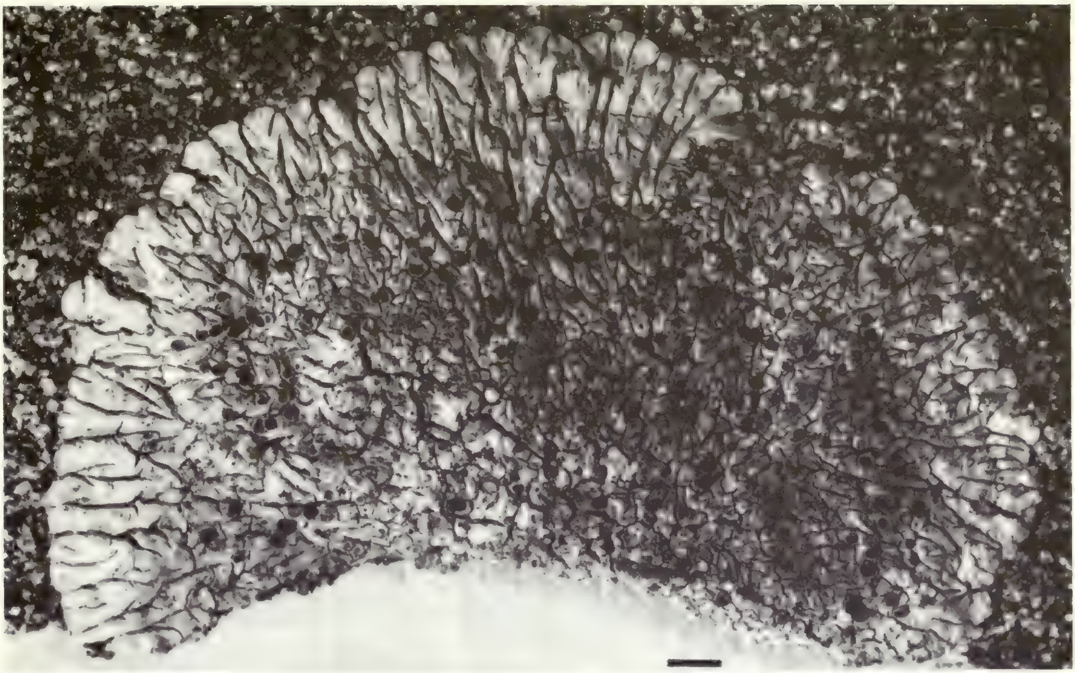

Fig. 22 Habit photograph of *Steinera radiata* subsp. *radiata* (holotype, BM). Scale = 2 mm.

Thallus *c.* 450 μm thick, upper zone pseudoparenchymatous, 60–90 μm thick, cell walls thin, well defined cells 18–25×15–20 μm, collapsed at the thallus surface to form a thin necrotic layer. Hyphae in algal zone thin-walled, cells 10–15×6–8 μm, algal filaments inspersed between the hyphal strands. Phycobiont a member of the Rivulariaceae, concentrated in a zone of *c.* 230 μm high, filaments 8–12 μm thick, discrete, contorted and folded, ± vertically aligned or radiating fan-wise near the lobe ends, intercalary and basal heterocysts present, ends of the filaments not distinctly tapered. Basal zone of thallus *c.* 140 μm thick, including scattered filaments of the alga, hyphae closely compacted, vertically to horizontally aligned according to their location at the centre or the margin of the thallus respectively, cells 10–16×4 μm, walls thickened, a few rhizoidal hyphae with darkened walls penetrating into the substrate.

Thecium *c.* 60 μm tall, epithecium red–brown appearing semi-opaque in thin sections. Asci 50–55×10–15 μm, elongate-clavate, broadest towards the apex, apex *c.* 6 μm thick with an amyloid cap. Spores 8 per ascus, simple, with a very thin and more or less median plasma-bridge but without a true transverse septum, shortly ellipsoid to subglobose, (7·5–) 8–10·5×(5·5–) 6·5–7·5 μm. Paraphyses rather sparse, more or less conglutinated in a gelatinous matrix, simple below, irregularly branched above, cells often irregular, apical cells to 7 μm, rounded. Margin compound, annular exciple well developed in old apothecia, to 0·1 mm broad, cells of radiating hyphae to 6–8 mm long. Subhymenium to 150 μm high, of short-celled hyphae interspersed by vertically aligned ascogenous hyphae in the upper part.

Specimen seen:
New Zealand: South Island, Fiordland, Mount Barber, above Deep Cove, *G. Einar & Greta Du Rietz* 2063:1 (type collection).

subsp. **aucklandica** P. James & Henssen, **subsp. nov.**
Figs 9A–G, 12B, 13E, 14A, 15A–B, 23B–E, 24.

A subsp. *radiata* ascis angustioribus, 55–60×8–12 μm, sporis longioribus ellipsoideis, (9·5–) 12–14 (15) × 3–4·5 (–5) μm, cellulis apicalibus paraphysium maioribus, usque ad 9 μm differt. Pycnidia in sectione 0·2 mm lata; conidia praecipue in lateribus formata, bacilliformia, 5 × 2μ, conidiophoris brevibus, articulatis.

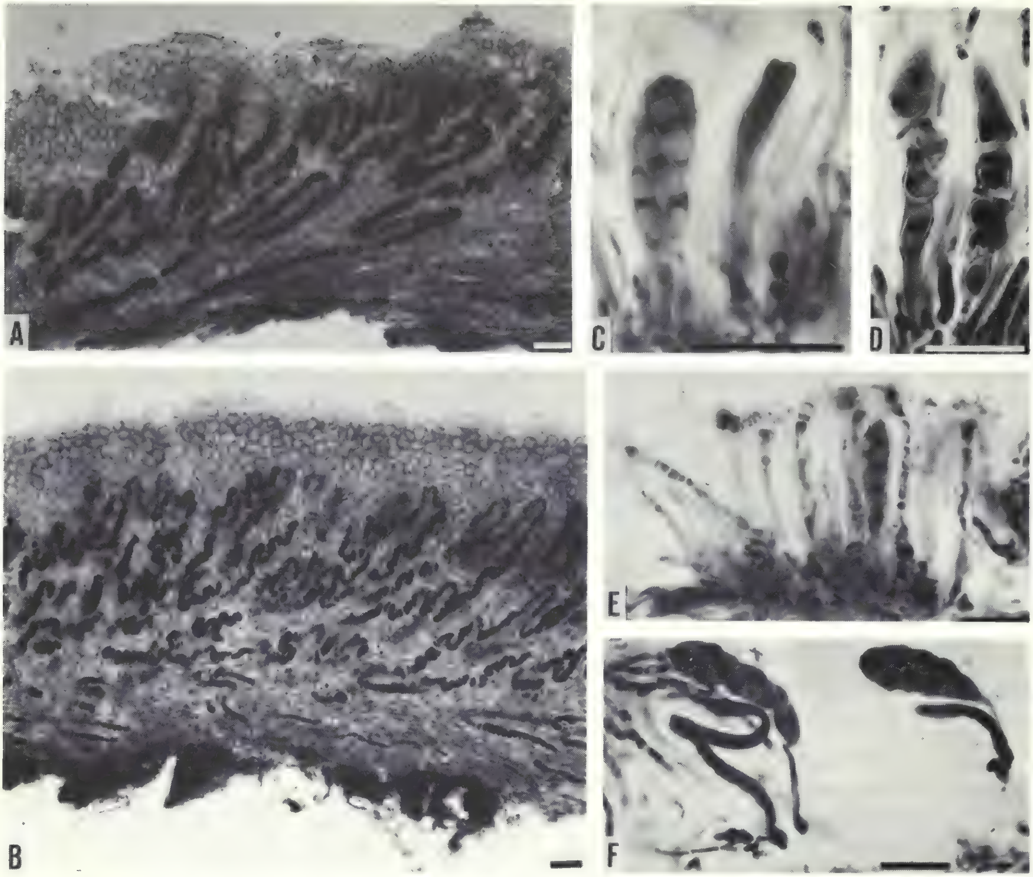

Fig. 23 Anatomy in *Steinera radiata* (both holotypes, BM). A *S. radiata* subsp. *radiata,* L.s. of thallus. B *S. radiata* subsp. *aucklandica,* L.s. of thallus. C–E *S. radiata* subsp. *aucklandica*, squash preparations showing spores and paraphyses; C Thickened apex of the ascus indicated by arrow; D Asci with deformed spores; E Submoniliform paraphyses. F *S. radiata* subsp. *radiata,* squash preparation of asci. Scale = 20 μm.

Typus: New Zealand: Auckland Islands, Auckland Island, Mount Eden. Ad saxa basaltica ferro abundantia in uliginosis inter caespites *Chionochlorae antarcticae* cum *Argopsis megalospora,* 320 m, 31 December 1962, *P. W. James* NZ 858/2 (BM—holotypus; CHR, MB—isotypi).

Similar to subsp. *radiata* in habit and anatomy, differing in the narrower, ellipsoid—clavate asci, 55–60×8–12 μm, and ellipsoid spores (9·5–) 12–14 (–15) 3–4·5 (–5) μm. Paraphyses often simple, less branched at the apices, and apical cells more noticeably swollen, up to 9 μm, than in subsp. *radiata*. Pycnidia numerous, inapparent, of the *Umbilicaria* type (see p. 000), 200×150 μm, outline rather irregular, convoluted, lined with short-celled conidiophores. Conidiogenous cells mainly producing conidia terminally. Conidia 5×2, rod shaped.

Specimens seen:
New Zealand: Auckland Islands, Auckland Island, Mount Eden, *P. W. James* NZ 858/2 (type collection); Auckland Island, Mount Eden, in small declivities on basalt rocks, with *Argopsis megalospora,* 340 m, 1 January 1963, *P. W. James* NZ 863/1 (BM).

Observations:
Steinera radiata is a very distinctive species, forming neat, rosette-shaped thalli with numerous emergent ascocarps, which at first are deeply immersed in the thallus. The species differs from

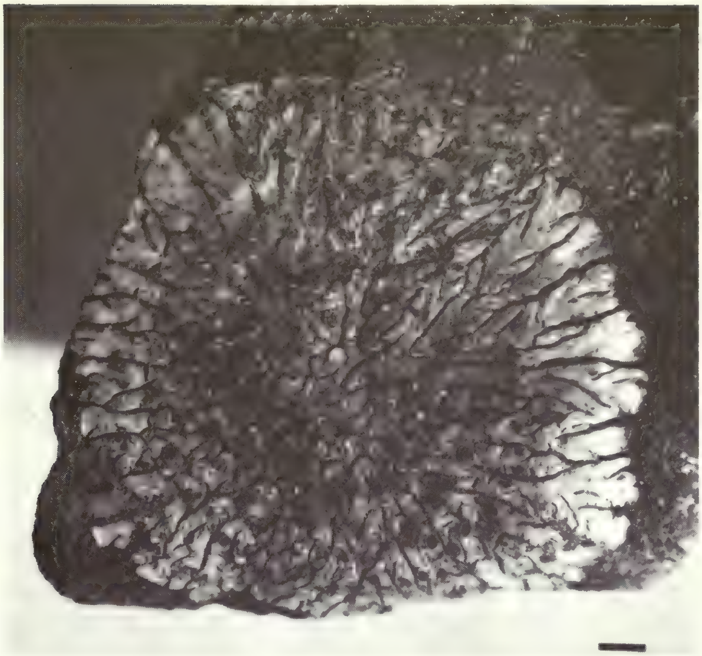

Fig. 24 Habit photograph of *Steinera radiata* subsp. *aucklandica* (holotype. BM). Scale = 2 mm.

other taxa in the genus in not having *Nostoc* as its phycobiont; the identity of the alga is, however, not known for certain but the presence of basal and intercalary heterocysts suggests that it belongs to the Rivulariaceae, even though the distal ends of the filaments are not tapered as is commonly found in this family.

In section, the apothecial margin of *S. radiata* is unusually (for the genus) well organized, and the ascocarps have a tendency toward the horizontal spread (Figs 10A–B, 11) which is characteristic of *Coccocarpia* and *Peltularia*.

Steinera radiata subsp. *aucklandia* is closely related to subsp. *radiata*. The two taxa are only separated by minor differences in the character of the spores, asci, and paraphyses (Fig. 13D–E). These differences may reflect the long isolation of the two subspecies.

Steinera radiata occupies a rather anomalous position in the genus. It differs from the other species in the simple spores, well developed excipulum proprium, low hymenium, lateral expansion of the apothecium, and the different phycobiont, all characters this species has in common with the monotypic genus *Peltularia*. Nevertheless, the placoid habit and the more or less homoiomerous organization of the thallus justify its inclusion in *Steinera*.

8. Methods

Unless otherwise stated the photographs of anatomical structures were prepared from freezing microtome sections mounted in lactophenol-cotton blue. All measurements are made from either squash preparations or microtome sections mounted in lactophenol-cotton blue.

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